INFLUENCES OF HUNTER HARVEST, TEMPERATURE, AND RELATIVE HUMIDITY ON NORTHERN BOBWHITE AND SCALED QUAIL IN THE ROLLING PLAINS OF TEXAS

A Dissertation

by

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ABSTRACT

The northern bobwhite (*Colinus virginianus)* has declined in abundance and range across much of its historic range. Although most biologists attribute this decline to habitat loss and change, many stakeholders perceive that hunting is partially responsible. I designed 3 studies to investigate the potential influence of both environmental factors and hunting in the Rolling Plains of Texas: (1) I examined the relationship of bobwhite abundance, and hunter effort to determine which of these best explains total harvest at statewide and regional scales; (2) I constructed a simulation model to examine the differences between heterogeneously and homogeneously applied bobwhite harvest to determine if traditional, homogeneous estimates of sustainable harvest overestimate sustainable harvest rates; and (3) I tested the hypothesis that native bunch grass vegetation apparently suitable for bobwhite nesting can act as thermal refugia for bobwhites to avoid harmful heat stress.

First, I determined which factors that influence total bobwhite harvest differed across Texas, but in the Rolling Plains both the abundance of bobwhites as well as the number of days hunters spend afield most strongly explained harvest. Because a measure of hunter effort factored so strongly, it was unlikely that current regulations could limit bobwhite harvest at small enough scales to prevent localized overharvest. In turn, such overharvest could lead to broad scale declines in bobwhite abundance and range, or accelerate ongoing declines. Second, I determined which harvest trends resulted in lower

landscape-level bobwhite density and range than under homogeneously applied harvest. Because harvest in the real world is applied heterogeneously and previously published sustainable harvest estimates relied on the assumption of homogeneously applied harvest pressure, it is likely that hunt managers harvest a larger proportion of the bobwhites on their property than they estimate. Finally, the ability to ameliorate heat stress was strongest during the late summer, when such nesting structures are at the peak of their growth cycle. Ultimately, range condition was strongly associated with both the magnitude of the temperature reduction and the duration of non-harmful temperatures. Thus, careful management of harvest and habitat are essential to maintain viable bobwhite subpopulations.

DEDICATION

For all my family, back to the beginning.

For Texas, her lands and people.

Díky Bohů za země zaslíbené—Texas.

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CHAPTER I

INTRODUCTION

Over 36% of gallinaceous bird species are threatened or endangered worldwide (IUCN 2013), and numbers are declining for at least 75% of the remaining species due to extensive habitat loss and fragmentation (Rands 1992). Although galliform harvest is of cultural and economic importance worldwide (McGowan et al. 2009), biologists have had little success determining the contribution of harvest to overall mortality within specific populations of various galliform species (Errington and Hamerstrom 1935, Roseberry 1979, Pollock et al. 1989, Keane et al. 2005, Sandercock et al. 2011). Furthermore, many harvested galliform species characterized by declining abundance exhibit limited dispersal ability, which increases their vulnerability to local overharvest in fragmented habitats (Collar et al. 1994). Overharvest in such habitats, in turn, could result in localized extinctions that contribute to broader-scale declining range and abundance for such species.

Vulnerability of galliform species characterized by limited dispersal ability to extirpation from localized overharvest in fragmented landscapes is of concern for conservationists worldwide. In North America, greater sage-grouse (*Centrocercus urophasianus*), ruffed grouse (*Bonasa umbellus*), and willow ptarmigan (*Lagopus lagopus*) exhibit a reduced ability to withstand harvest when sub-populations lose connectivity through habitat change, thereby contributing to population decline (Small et al. 1991, Gibson 1998, Smith and Willebrand 1999, Connelly et al. 2003, Hörnell-Willebrand et al. 2014). In Europe, Scotland banned all capercallie (*Tetrao urogallus*)

hunting in 2001 in the face of rapidly changing landscapes (Scottish Government 2001). Regulatory agencies closed harvest within remnant populations for several species in fragmented habitat, including the greater sage-grouse, greater prairie chicken (*Tympanuchus cupido pinnatus*), and lesser prairie chicken (*T. pallidicinctus*) because harvest could contribute to extinction risk (Johnson and Braun 1999, Silvy and Hagen 2004). Although responses of galliform populations to habitat fragmentation have been modeled (Beissinger and McCullough 2002, Akçakaya et al. 2004, Beissinger et al. 2006, Blomberg et al. 2012), none of these models explicitly considered the interacting effect of harvest with habitat fragmentation. In addition to fragmented habitat, one may conclude that harvest effort is not homogeneously applied across the range of such harvested galliform species during hunting seasons. Thus, it is possible that disproportionately high harvest in areas where galliform populations are threatened by marginal habitat can exceed local extinction thresholds, thereby accelerating already-steep declining abundance and range of a species by decreasing connectivity among subpopulations.

Northern bobwhites (*Colinus virginianus*; hereafter bobwhite) in the state of Texas, USA are an excellent model of harvested galliforms whose survival may be negatively influenced by the interaction of harvest and environmental factors. Bobwhites have declined in abundance over large spatial areas since at least the 1960s and perhaps for more than 100 years (Leopold 1931, Peterson et al. 2002, Sauer et al. 2012). The source of this marked decline in abundance has been greatly debated by biologists, hunters, landowners, and other stakeholders. Most biologists, however, agree that habitat

loss, fragmentation, and degradation, rather than harvest, is the primary cause of declining bobwhite abundance and range (e.g., Roseberry and Klimstra 1984, Peterson 2001, Williams et al. 2004). Regardless, stakeholders continue to express concerns over the influence of hunting on bobwhites, perhaps because declines are most often noted during the hunting season when comparing quarry encounter rates with previous years' hunting successes (Texas Parks and Wildlife Commission 2012). Although a number of studies conducted across the range of the bobwhite attempted to estimate sustainable harvest for bobwhites, estimates range from 0 to 70% of bobwhites in a given area (Leopold 1933, Vance and Ellis 1972, Roseberry 1979, Roseberry et al. 1979, Shupe 1987, Sands 2010, Guthery 2012). With such marked variability in estimated sustainable harvest, it seems that other factors likely contribute to the severity of the deleterious effects of harvest.

Current bobwhite harvest regulations in Texas are based on the model of "self-regulatory" harvest (Peterson and Perez 2000), which presumes that harvest managers on individual properties accurately scale harvest to fluctuating bobwhite abundance. Such assumptions, however, are based on data collected at the level of an entire state, whereas bobwhite hunting occurs at the level of individual pastures (Williams et al. 2004). Because hunting is not homogeneously conducted across at either the regional or statewide scale, it is reasonable to assume that finer-scale relationships between hunting and bobwhite population dynamics may not be accurately reflected in broad-scale estimates. Because bobwhites are a species characterized by limited dispersal ability (Duck 1943, Baumgartner 1944, Madison 1998, Taylor et al. 1999, Liu et al. 2002,

Townsend et al. 2003, Terhune et al. 2010), it is possible that habitat loss, fragmentation, and degradation can interact with hunting to exceed localized extinction thresholds, thereby accelerating trends of declining abundance or range.

The Rolling Plains of northwestern Texas (Gould 1969) are an excellent system to examine the potentially harmful influences of both harvest and environmental factors on the viability of northern bobwhite remnant populations for several reasons. This region historically has been an area where extensive bobwhite hunting is an economically important activity (Conner 2007), with data on bobwhite demography and hunter success collected at several TPWD wildlife management areas, as well as long roadside routes over many years (Jackson 1969, Purvis 2012). Despite such an ample supply of bobwhite and hunters, little is known about the driving factors of bobwhite harvest in this region of Texas, or its sustainability as bobwhite abundance and range continue to decline. Curiously, no estimates of sustainable harvest have been made for bobwhites in the Rolling Plains of Texas, despite available data, and its perceived status as one of the last bastions of huntable, wild bobwhite subpopulations.

Quail biologists have long recognized that environmental factors, such as extreme cold (Robinson and Baker 1955), prolonged ice and snow coverage (Roseberry 1964, Klimstra and Roseberry 1975), flooding (Stoddard 1931, Lehmann 1984), and extreme heat (Johnson and Guthery 1988, Forrester et al. 1998, Guthery et al. 2005b) limit bobwhite production and survival. Earlier research provided ancillary evidence regarding the importance of thermal refugia for bobwhites in semi-arid ecosystems on the western edge of the bobwhite's range (Hernández and Peterson 2007), such as the

Rolling Plains, extreme heat is one common environmental factor that can render otherwise-usable habitat inhospitable, cause asynchronous incubation, kill adults, and stunt or kill embryos, thereby severely limiting bobwhite production (Guthery et al. 2001, Reyna 2010, Reyna and Burggren 2012). Further, broad scale weather phenomena that influence the production of nesting vegetation (e.g., precipitation, temperature) could explain a large proportion of the variability in bobwhite abundance among years (Lehmann 1984, Bridges et al. 2001, Guthery et al. 2002, Lusk et al. 2002).

Bobwhites often select nest sites in vegetation (i.e., native bunch grasses) that likely maintains cooler microclimates through the interaction of sun-shading and evaporative cooling (Johnson and Guthery 1988, Guthery et al. 2005b, Hernández and Peterson 2007, Rader et al. 2007). As a result, these vegetative structures may be essential components of bobwhite habitat in their ability to ameliorate detrimental effects of harmful weather, including heat. Drought and livestock grazing, however, often limit the availability of such vegetation in semi-arid regions, thereby reducing potential bobwhite production (Bridges et al. 2001, Guthery et al. 2002). Laboratory studies quantified the relationship between heat stress, reduced immunocompetence of adults, developmental plasticity, and embryo death (Dabbert et al. 1997, Reyna 2010, Reyna and Burggren 2012). Thus, lack of thermal refugia due to drought, heavy livestock grazing, or other land uses that consumes or degrades essential vegetation, reduces available habit and therefore may lower the landscape carrying capacity below levels required for viable bobwhite subpopulations (Forrester et al. 1998, Guthery 1999, Guthery et al. 2000). A few field studies attempted to quantify heat experienced by wild

bobwhites, but were limited by small spatial and temporal extent, and did not address nesting structures (e.g., Forrester et al. 1998, Guthery et al. 2001, Guthery et al. 2005b).

Although hunting is not considered to be a driving force in reductions in bobwhite abundance and range, it may magnify the effects of environmental factors that fragment bobwhite habitat in ways imperceptible to the human eye. Thus, it is likely that such an interaction between environmental factors that reduce usable space (sensu Guthery 1999) for bobwhites and harvest contribute to localized reductions in bobwhite abundance and/or range in the Rolling Plains of Texas. In turn, such reductions may contribute to range-wide declines in abundance and range by interrupting metapopulation dynamics critical to the viability of bobwhite populations. Recently, various levels of Texas government initiated an effort to address the declining range and abundance of bobwhites. For any such endeavor to be successful, however, it must first understand the factors driving these declines. Thus it is critical to identify which aspects of harvest and environmental factors may contribute to declining abundance and range of northern bobwhites in Texas.

In the course of this study, I identified various aspects of harvest and environmental stress that may directly contribute to the continued declining abundance and range of bobwhites in Texas. Specifically, I investigated 3 aspects of the influence of harvest and environmental factors on bobwhites in the Rolling Plains of Texas: (1) I examine the relationship of bobwhite abundance, and several measures of hunter effort on harvest to determine which of these best explained total harvest at statewide and regional scales in Texas; (2) I construct a simulation model to examine the differences

between heterogeneously and homogeneously applied bobwhite harvest pressure on bobwhite abundance and range at the landscape level to determine if traditional estimates of sustainable harvest, which rely on the assumption of homogeneous harvest application, overestimate sustainable harvest rates; and (3) I examine the potential influence of heat as an environmental factor whose effect on bobwhites may limit usable habitat if native bunch grass vegetation apparently suitable for bobwhite nesting cannot sufficiently reduce heat experienced *in situ* for bobwhites eggs to avoid harmful heat stress. I end by interrelating these 3 aspects, their potential interactions and subsequent effects on bobwhites populations in the Rolling Plains of Texas, and provide recommendations for those seeking to halt or reverse the current trend in the declining abundance and range of bobwhites.

CHAPTER II

QUAIL ABUNDANCE, HUNTER EFFORT, AND HARVEST OF 2 TEXAS QUAIL SPECIES: IMPLICATIONS FOR HUNTING MANAGEMENT

Synopsis

Managing exploited species characterized by declining abundance, such as northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*), presents challenges for regulatory agencies and wildlife managers. My objective was to determine the influence of quail abundance and quail hunter effort on annual bobwhite and scaled quail harvest in Texas, USA, as a model for similar species. I formulated competing models accounting for quail harvest at both statewide and regional scales using hunter survey and quail abundance data collected by the TPWD (1978–2012) and evaluated them using multiple linear regression and model selection (AICc). Statewide bobwhite and scaled quail harvest was best predicted by models that included quail abundance, quail hunter-days or total quail hunters, respectively (R^2 = 0.969 and 0.915, respectively). My most plausible models also predicted regional quail harvest reasonably well ($R^2 \geq 0.67$), but in some regions diverged from statewide models, with hunter effort alone best explaining quail harvest. Despite my models' high predictive ability, current hunting regulations do not reflect variability in factors driving harvest at the spatial scales I evaluated. Species characterized by limited dispersal ability, such as quails, are at risk of localized overharvest when hunting management cannot limit harvest at the same spatial scale where hunting occurs. For Texas quails, harvest management implemented by individual property managers, rather than statewide hunting regulations,

is the most appropriate way to avoid localized overharvest because property managers can control harvest at the scale relevant to both quails and quail hunters.

Introduction

Management of exploited wildlife species presents difficulties for those tasked by statute with their conservation, particularly when abundance of these species has declined for decades and numbers fluctuate markedly among years. Stakeholders often perceive short-term (3–5 year) swings in abundance as proof that the long-term decline in abundance is markedly worsening or improving when neither conclusion is justified. Despite the fact that limiting hunting season length, bag limits, and/or means and methods contributed to the restoration of some exploited species (Leopold 1933, Allen 1954, Rosene 1969, Ayal and Baharav 1983, deCalesta 1983, Miller 1990), others still experienced long-term declines in abundance and range extent despite these measures (Marboutin and Peroux 1995, Johnson and Braun 1999, Silvy and Hagen 2004). Harvest management for 2 New World quail species, northern bobwhite (*Colinus virginianus;* hereafter bobwhite) and scaled quail (*Callipepla squamata*), in the United States epitomizes this situation. Bobwhite, once one of the most common and widely hunted North American gamebird species, has declined in abundance over large spatial areas since at least the 1960s and perhaps for more than 100 years; scaled quail abundance has declined for several decades, especially in the State of Texas, USA (Leopold 1931, Peterson et al. 2002, Merola-Zwartjes 2005, Sauer et al. 2012). Although most quail biologists agree that habitat loss, fragmentation, and degradation, rather than harvest, are the primary causes of declining bobwhite and scaled quail abundance and range (e.g.,

Roseberry and Klimstra 1984, Peterson 2001, Williams et al. 2004), there is considerable stakeholder pressure to alter hunting regulations in an attempt to halt or reverse these long-term trends (Godfrey 2012, Simms 2012, Texas Parks and Wildlife Commission 2012).

Quail hunting opportunities are readily available in Texas for those who can afford hunting leases on private property. Most hunters hunt with shotguns over dogs, bounded by a season between late October and late February, with a statewide daily bag limit of 15 birds. Because few hunters hunt the entire season, and fewer still fill a daily bag limit, quail hunting in Texas is functionally unregulated, except by land managers or hunters themselves (Peterson and Perez 2000, Peterson 2001). Peterson and Perez (2000) demonstrated that both bobwhite and scaled quail hunting in Texas was consistent with the hypothesis that quail hunting was largely self-regulatory (hunter effort responds to fluctuations in quail abundance). This relationship seems clear when one compares the long-term trends for statewide and regional quail abundance and hunter effort (Figs. A2-1–4). Peterson and Perez (2000) maintained that hunters expended less time hunting quail (i.e., spent few days afield or did not hunt at all) during low as opposed to high quail abundance years. Guthery et al. (2004a) examined roadside surveys and harvest data for bobwhites in the States of Oklahoma and Missouri, USA, concluding that bobwhite hunting was not self-regulatory at low quail densities. The ratio of hunters to bobwhites tended to increase as bobwhite and hunter numbers decreased, and the remaining hunters harvested a greater proportion of remaining bobwhites than in times of greater abundance due to increased hunter efficiency (birds killed per hunter per day).

Thus, the number of birds harvested would be disproportionate to the number of hunters afield and quail abundance. Guthery et al. (2004b) reported similar results for bobwhites, scaled quail, and Gambel's quail (*Callipepla gambelii*) using data from Arizona, Kansas, Missouri, Oklahoma, and Texas, USA. Regardless, both the self-regulatory (Peterson and Perez 2000) and differential hunter efficiency (Guthery et al. 2004a, Guthery et al. 2004b) explanations predict that modestly restrictive daily bag limits (e.g., 5–7 birds) may be too conservative when quail are abundant, yet too liberal when quail are scarce (Peterson 2001). Whereas both explanations suggest that restrictive fixed daily bag limits (e.g., 2–3 birds) and/or major reductions in season length (e.g., 1–2 week season) may indeed prevent overharvest during periods of low quail abundance, Peterson (2001) and Guthery et al. (2004a, 2004b) asserted that many quail hunters are unlikely to view such restrictive changes favorably.

Although many factors (e.g., access, weather) influence quail harvest, a clear understanding of both quail abundance and hunter effort is required to achieve harvest objectives. Although quail biology has been studied in detail, the contribution of hunter effort to quail harvest has received less attention. Texas presents an excellent opportunity for clarifying the influence of the quail abundance and hunter effort on quail harvest for 4 primary reasons. First, bobwhite and scaled quail occur both allopatrically and sympatrically in Texas, with one or both species occupying portions of all 10 ecological regions of the state (Fig. A2-5; Gould 1969, Hernández and Peterson 2007, Silvy et al. 2007). Second, Texas Parks and Wildlife Department (TPWD) used identical methods for monitoring abundance and harvest for these species since 1978 (Peterson

and Perez 2000, Purvis 2012). Third, the abundance of bobwhite and scaled quail has declined for many years, primarily due habitat conversion and loss (Brennan 1991, Bridges et al. 2002, Lusk et al. 2002, Merola-Zwartjes 2005), with marked fluctuations in abundance among years due to environmental stochasticity (Bridges et al. 2001, Lusk et al. 2007). Finally, stakeholders recently demonstrated a continued belief that minor changes to hunting regulations could halt or reverse the decline in quail abundance in Texas (Texas Parks and Wildlife Commission 2012).

My objective was to determine the influence of quail abundance and quail hunter effort on annual total harvest of bobwhites and scaled quail in Texas. I explored how localized overharvest can contribute to declining abundance and range extent of quails and similar exploited species characterized by limited dispersal ability. I end with suggestions for managing harvest for such species more effectively.

Methods

I modeled total annual bobwhite and scaled quail harvest using quail abundance and harvest data from TPWD roadside counts (1978–2012) and the TPWD *Small Game Harvest Survey Results* (1981–1983 and 1986–2012), respectively. TPWD staff biologists survey these 32.2km (20 mile) transects at sunrise (east-to-west) or 1 hour before sunset (west-to-east) each August at a rate of 32.2 km/hour (20 mph), and record the number of quail seen on every 1.6 km of road (1 mile). Peterson and Perez (2000) detail the design and history of these surveys and incongruity of survey years. I used counts of abundance from 162 TPWD roadside survey routes in the High Plains, Rolling Plains, Edwards Plateau, South Texas Plains, Gulf Prairies, Cross Timbers, and Trans-

Pecos ecological regions of Texas (Fig. A2-5; Gould 1969). I did not include data from the remaining 3 ecological regions (i.e., Pineywoods, Post Oak Savannah, and Blackland Prairies) because TPWD discontinued quail surveys for these regions in 1988. I used hunter harvest survey data for the same 7 ecological regions (182 counties). I first pooled these data at the statewide level for analysis to reflect the scale at which hunting is currently regulated. I then analyzed these data at the ecological region level for each species to determine whether there were differences between the hunting of bobwhites and scaled quail at statewide and regional scales.

I developed a series of competing models, using multiple linear regression, with the total number of bobwhite or scaled quail harvested per year (hereafter total quail harvest) as the dependent variable in all models. Because quail harvest cannot occur without both quarry and hunters, my independent variables represented these factors. Specifically, I used the mean number of bobwhites or scaled quail observed on each August survey route (hereafter quail abundance) to represent quail abundance and the total number of quail hunters (hereafter total quail hunters), and the total number of days hunters spent afield hunting quail (hereafter quail hunter-days) to represent hunter behavior. These variables representing hunter effort included all hunters, regardless of hunting success. Although the summary of annual *Small Game Harvest Survey Results* (Purvis 2012) includes the mean number of birds harvested per hunter per day calculated from other variables, only total quail harvest, total quail hunters, and quail hunter-days are provided by respondents, so I used only these 3 variables in my models.

Because these count data are Poisson distributed, I log-transformed each variable (Zar 2010), and using normal probability plots found transformed data were normally distributed. Because it is reasonable to assume that harvest survey variables could be related, I tested for multicollinearity among these variables using the variance inflation factor (VIF; Neter et al. 1996). Total quail hunters and quail hunter-days were highly collinear (VIF = 21.09–53.55), so I restricted these variables to separate regression models, and thus did not provide a global model in my candidate model set. My candidate models included all other combinations of quail abundance, total quail hunters, and quail hunter-days. Because quail hunters alter participation and effort due to changes in quail abundance harvest (Peterson and Perez 2000, Guthery et al. 2004a), I also modeled the interaction between quail abundance and total quail hunters or quail hunter-days. Residual plots for all analyses were randomly distributed. I ran all models separately for bobwhites and scaled quail using JMP Pro 11.0.0 (SAS 2013), and selected among candidate models using Akaike's information criterion corrected for small sample size (AICc). Models were considered plausible if they were within the 95% confidence set of models ($\Sigma\ W_i \geq 0.95$). I did not present models that included interaction terms if the model added 1 parameter (interaction term) and had a -2 log likelihood (-2LnL) similar to, and the Δ_i was within 2 units of the model without the interaction (Burnham and Anderson 2002; p 131). I included coefficients of determination (R^2) in tables so that I could determine how much of the total variability in the data was explained by plausible models (Guthery et al. 2005a).

Results

Statewide bobwhite harvest in Texas was best accounted for by the model that included quail abundance and quail hunter-days (Table A1-1). The model including quail abundance and total quail hunters also was plausible, but was 5.65 times less likely to be the best-supported model among those evaluated than the best-supported model based on evidence ratios (ω_1/ω_i; Table A1-1). None of the models including interactions were plausible. The only plausible model for scaled quail harvest at the statewide level included quail abundance and total quail hunters (Table A1-2). Interestingly, all models evaluated did a reasonably good job of accounting for the variability in bobwhite and scaled quail harvest among years ($R^2 \geq 0.830$; Table A1-1, and $R^2 \geq 0.672$; Table A1-2, respectively), despite the fact that some did a much better than others.

The most plausible model for bobwhite harvest in the Rolling Plains included quail abundance and hunter-days, with and without the interaction term, although the model that incorporated quail abundance and total quail hunters also was plausible (A1-3). The best-supported models for bobwhite harvest in the High Plains, Gulf Coast Prairies, and Cross Timbers incorporated quail abundance and total quail hunters, but the model including quail abundance and quail hunter-days also was plausible for the Gulf Coast Prairies, as in the Rolling Plains. Although bobwhite harvest in the Edwards Plateau and South Texas Plains was best accounted for by the model that considered only hunter-days, as in other regions, the next most plausible models for both regions included quail abundance.

Scaled quail harvest in the High Plains and Edwards Plateau was best accounted for by models that included quail abundance and total quail hunters (Table A1-4). In the Trans-Pecos, the most plausible model included quail abundance and quail hunter-days, but the model including only quail hunter-days also was plausible. The model that included only total quail hunters best explained scaled quail harvest in the Rolling and South Texas Plains, although models that considered quail abundance and total quail hunters also were plausible.

Discussion

I found that quail abundance and hunter effort (total hunter-days and total hunters) accounted for 96.9 and 91.5% of the variability in statewide bobwhite and scaled quail harvest in Texas, respectively. In fact, all models that included both quail abundance and a measure of hunter effort accounted well for quail harvest ($R^2 \geq 0.871$; Tables A1-1–A1-2). These results are consistent with the self-regulatory explanation of quail harvest at the statewide scale (Peterson and Perez 2000), as all plausible models included quail abundance and reflected the influence of hunter effort–quail hunter-days, and to a lesser extent total quail hunters–on total bobwhite harvest, or the number of people hunting 1 or more days on total scaled quail harvest. The difference between the measure of hunter effort for the species may be the result of scaled quail hunters hunting the same number of days during a given hunting season, whereas some bobwhite hunters may hunt many more days than others due to factors such as expensive hunting rights leases (Conner 2007).

At the ecoregion scale, similar models were most plausible for bobwhites in the High Plains, Rolling Plains, Gulf Coast Prairies, and Cross Timbers, and for scaled quail in the High Plains, Edwards Plateau, and Trans-Pecos. In all these cases, quail abundance and a measure of hunter effort accounted for ≥ 67.9% (Tables A1-3–A1-4) of the variation in quail harvest. Divergence occurred from statewide models in regions, such as the Trans-Pecos, where quail abundance and hunter-days best explained quail harvest, rather than total quail hunters. This is likely because scaled quail are not typically hunted coincidental to bobwhites in this region, as they are in others. Interestingly, hunter effort alone accounted for ≥82.6% in some regions (i.e., South Texas Plains, Edwards Plateau for bobwhites; Rolling Plains and South Texas Plains for scaled quail). The lack of quail abundance in most plausible models for the Rolling and South Texas Plains may be due to lucrative quail fee-hunting operations that dominate quail harvest in these regions; lessees pay so much for hunting access that they may hunt regardless of abundance (Conner 2007). Further, if quail harvest is best explained by hunter effort alone, lower quail abundance would not necessarily regulate harvest, contrary to the self-regulatory explanation of quail harvest (Peterson and Perez 2000). Thus, those formulating hunting regulations should consider variability in quail abundance as well as specific measures of hunter effort.

Current statewide quail hunting regulations cannot address variability in either quail demographic parameters or most quail hunter behaviors that drive harvest in Texas. Thus, I concur with earlier studies that concluded minor changes in statewide hunting regulations are unlikely to reduce harvest (Peterson and Perez 2000, Peterson 2001,

Guthery et al. 2004a, Guthery et al. 2004b). Regardless, some stakeholders continue to believe that minor reductions in daily bag limits (i.e., 1–2 birds lower) or season lengths (i.e., 1–2 weeks shorter) could halt or reverse declining quail abundance in Texas (Sasser 2012). Other researchers maintained that, although more draconian reductions in daily bag limits and/or season lengths probably would reduce statewide quail harvest when birds are abundant, they are much less likely to be effective when quail numbers are low (Peterson 2001, Guthery et al. 2004a). Possibly for these reasons, some stakeholders in Texas recently argued for more extreme changes to hunting regulations, such as a statewide closed season (Texas Parks and Wildlife Commission 2012).

Quail biologists long have been aware of bobwhite vulnerability to localized overharvest (Roseberry et al. 1979, Williams et al. 2004), yet no one has analyzed the influence of spatially heterogeneous quail harvest, despite Roseberry's (1991) call for such research. Ignoring the spatial aspects of quail ecology results in hunting regulations that may limit some aspects hunter effort across a state, but do not limit hunter take within quail subpopulations in any measurable way. For this reason, current bobwhite and scaled quail hunting regulations in Texas cannot limit hunter effort or annual harvest at the regional scale, much less the spatial scale relevant to quail and quail hunters (i.e., the pasture; Williams et al. 2004), even if minor adjustments are made to reflect fluctuations in abundance statewide and certain aspects of hunter effort that influence each species. Thus, overharvest on individual properties can produce localized extirpations that may accelerate broad scale declines in abundance or range extent for

any metapopulation where emigration and immigration cannot easily occur, while still operating within statewide hunting regulations.

For Texas quails, a number of solutions may be effective to prevent localized overharvest, including spatially explicit hunting regulations already employed for similar galliform species characterized by declining abundance and range extent (e.g., Williams et al. 2004, California Department of Fish and Wildlife 2013, South Dakota Department of Game Fish and Parks 2014). These solutions could include marked reductions in statewide season lengths and bag limits (Peterson 2001), replacing daily bag limits with annual quotas (Andersen et al. 2014), regulating season lengths and bag limits at the ecoregion or finer scale (Williams et al. 2004), or even closing the quail hunting season statewide, except on individual properties (including cooperatives) that maintain habitat demonstrated to be suitable to support hunted subpopulations (Guthery et al. 2000), thereby effectively managing harvest at the pasture scale. Under any regulatory option, aside from closing the season or issuing individual property hunting permits, localized overharvest can still occur. Therefore, the most effective way to prevent localized overharvest in a private-land state such as (≥97% privately owned; Wilkins et al. 2009), lies with those who functionally manage harvest at the scale relevant to both quail and quail hunters: the individual hunting property manager. Therefore, I recommend that regulatory agencies and other wildlife professionals promote awareness of the potential for and effects of localized overharvest, and help land managers develop strategies to avoid this potential consequence of hunting.

The implications of localized overharvest extend beyond Texas quails: vulnerability of species characterized by limited dispersal ability to extirpation from localized overharvest is of concern for conservationists worldwide. In North America, greater sage-grouse (*Centrocercus urophasianus*), ruffed grouse (*Bonasa umbellus*), and willow ptarmigan (*Lagopus lagopus*) exhibit a reduced ability to withstand harvest when sub-populations lose connectivity through habitat change, thereby contributing to population decline (Small et al. 1991, Gibson 1998, Smith and Willebrand 1999, Connelly et al. 2003, Hörnell-Willebrand et al. 2014). In Europe, Scotland banned all capercallie (*Tetrao urogallus*) hunting in 2001 in the face of rapidly changing landscapes (Scottish Government 2001). Recently, a nation-wide, multi-year survey in Scotland concluded that the spatial ramifications of mountain hare (*Lepus timidus*) harvest warranted further investigation (Kinrade et al. 2008). Similar concern has been expressed for the brown hare (*Lepus europaeus*) in Denmark, as changing agricultural landscapes effectively isolated subpopulations (Jensen 2009). In South America, concern has been directed toward subsistence hunting of many Amazonian vertebrates exhibiting various levels of limited dispersal ability in increasingly fragmented landscapes (Peres 2001). Clearly, those seeking to conserve exploited species characterized by limited dispersal ability in fragmented habitats are beginning to address vulnerability to localized harvest.

Conclusions

Given the potential biological and political ramifications of changes in hunting regulations, wildlife policy makers must ensure their perceptions of hunting regulations

match regulations' ability to influence quail harvest. My models that included both quail abundance and some measure of hunter effort explained nearly all variability in statewide bobwhite and scaled quail harvest among years in Texas, but the specific measure of hunter effort was different in some regions. Further, quail harvest in some regions was best predicted by hunter effort alone. Thus, most regulatory changes are unlikely influence quail abundance. Although adding large expanses of contiguous habitat would certainly be the best action to reverse declining abundance of such species, harvest management strategies must function at a scale relevant to the species and its hunters to avoid accelerating declines of these limited dispersal species through localized overharvest. For Texas quails, harvest management by individual property managers, not statewide hunting regulations, are the best way to avoid localized overharvest. Due to the long-term decline in bobwhite and scaled quail, there is a critical need for wildlife professionals and hunting property managers to engage in a dialogue regarding the array of management strategies that could prevent localized overharvest.

CHAPTER III

SIMULATING THE EFFECTS OF SPATIALLY HETEROGENEOUS HARVEST ON NORTHERN BOBWHITES

Synopsis

Galliformes are exploited worldwide, yet over one-third of gallinaceous bird species are threatened or endangered (IUCN, 2013). Current harvest models reflect neither the spatial structure of exploited populations nor the spatial distribution of the harvest. I developed a spatially-explicit model to simulate recruitment, dispersal, and mortality of northern bobwhites (*Colinus virginianus*) assuming spatially heterogeneous versus homogeneous harvest. I parameterized the model to represent ranch (hunting management unit) sizes and configurations representative of Cottle County, Texas, a portion of the Rolling Plains ecological region with long-term demographic data for bobwhite populations. Simulated densities (bobwhites/ha) and ranges (number of 1-km^2 patches with > 1 bobwhite) were significantly lower when harvest was distributed heterogeneously rather than homogeneously among ranches for mean harvest levels up to but not including 60% ($df = 999$, $P < 0.001$). Thus models that do not reflect the spatial structure of exploited populations and the spatial distribution of the harvest may overestimate sustainable harvest, especially for gallinaceous species with limited dispersal ability, such as bobwhites.

Introduction

Although galliform harvest is of cultural and economic importance worldwide (McGowan et al. 2009), biologists have had little success determining the contribution of harvest to overall mortality within specific populations (Errington and Hamerstrom Jr 1935, Roseberry 1979, Pollock et al. 1989, Keane et al. 2005, Sandercock et al. 2011). Over 36% of gallinaceous bird species are threatened or endangered (IUCN 2013), and numbers are declining for at least 75% of the remaining species due to extensive habitat loss and fragmentation (Rands 1992). Many galliform populations characterized by declining abundance exhibit limited dispersal ability, which increases their vulnerability to local overharvest in fragmented habitats (Collar et al. 1994). Regulatory agencies closed harvest within remnant populations for several species in fragmented habitat, including the greater sage-grouse (*Centrocercus urophasianus*), greater prairie chicken (*Tympanuchus cupido pinnatus*), and lesser prairie chicken (*T. pallidicinctus*) because harvest could contribute to extinction risk (Johnson and Braun 1999, Silvy and Hagen 2004). Although responses of galliform populations to habitat fragmentation have been modeled (Beissinger and McCullough 2002, Akçakaya et al. 2004, Beissinger et al. 2006, Blomberg et al. 2012), none of these models explicitly considered the effect of spatially heterogeneous harvest.

The northern bobwhite (*Colinus virginianus;* hereafter bobwhite) is a harvested galliform of economic importance in agricultural and natural systems (Stoddard 1931, Burger et al. 1999, Guthery 2002, Conner 2007) whose abundance has declined extensively for over 100 years, primarily due to habitat loss (Leopold 1931, Church et al.

1993, Bridges et al. 2002, Peterson et al. 2002, Lohr et al. 2011, Halley et al. 2014). Although bobwhites still are harvested across their range, populations exist primarily as isolated remnants in fragmented habitat, except in certain regions of Kansas, Missouri, Oklahoma, and Texas, USA. (Droege and Sauer 1990, Church et al. 1993, Sauer et al. 2012). Harvest of bobwhites in fragmented habitat increases extinction risk compared to unharvested populations (Guthery et al. 2000), although it is not considered the primary contributor to the range-wide decline in abundance (Peterson 2001). Research addressing the contribution of harvest to overall mortality has yielded estimates of sustainable harvest levels ranging from 0 to 70% (Leopold 1933, Vance and Ellis 1972, Roseberry 1979, Roseberry et al. 1979, Shupe 1987, Sands 2010, Guthery 2012). Without well-defined and sustainable harvest strategies, local managers regulate harvest based on personal experience, creating a patchwork of harvest and habitat management regimes across the species' range (Clement 2003, Williams et al. 2004). Increasing evidence suggests that sustained-percentage harvest of highly spatially-structured populations in fragmented habitats may be unsustainable (McCullough 1996) due to unknown local extinction thresholds (Bascompte and Sole 1996). Although Roseberry (1991) called for landscape scale studies of bobwhite population responses to harvest, harvest models continue to focus on closed populations subjected to spatially uniform harvest rates.

In this study, I explored the effects of assuming spatially heterogeneous versus homogeneous harvest on estimates of bobwhite densities (birds/ha) and ranges (number of 1-km^2 patches with >1 bird) that could be sustained under each of several mean harvest levels. I first described a spatially-explicit model that simulates recruitment,

dispersal, and harvest and non-harvest mortality of bobwhites within a heterogeneous landscape. I then simulated scenarios in which mean harvest levels ranging from 10 to 70% were distributed heterogeneously versus homogeneously across the landscape. I conclude with implications of my findings for estimating sustainable harvest of bobwhites and other gallinaceous species with limited dispersal ability.

Study Area

I parameterized my model to represent Cottle County, in the Rolling Plains of Texas, USA (Gould 1969), a semi-arid region that supports large, but declining, bobwhite populations critical to the regional economy (Jackson 1969, Brennan 2007). Average annual precipitation varies between 561and 762mm. Mean summer temperatures range between 21 and 36 °C, with mean winter temperatures of -16–15°C. There is a summer dry period with increased temperature and evaporation rates. Elevation ranges from 250 to 910 m. Soils vary from coarse sands to tight, hard clays. Vegetation communities were historically dominated by mid- to tall-grass species including little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), sand bluestem (*A. hallii)*, Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), Canada wildrye (*Elymus canadensis*), and western wheatgrass (*Pascopyrum smithii*). Riparian areas supported woody plant communities that included oaks (*Quercus spp.),* eastern cottonwood (*Populus delitoides*), elms (*Ulmus spp.*), junipers (*Juniperus spp.*), and honey mesquite (*Prosopis glandulosa*). More recently, extensive brush encroachment related to overgrazing has resulted in reduction of grass-dominated range sites. Approximately

40% of the land area has been cultivated, primarily in cotton and wheat, with almost all remaining rangeland managed for beef cattle production and fee hunting; <1% of the study area was urbanized (USDA-NASS 2007).

Methods

Model Description

The model, which is stochastic, agent-based, and programmed in NetLogo© 5.0.1 (Wilensky 1999), simulates recruitment, dispersal, and harvest and non-harvest mortality of bobwhites on a 693-km^2 area typical of the Rolling Plains of northern Texas (Fig. A2-6). The simulated landscape is divided into 1 km^2 patches arrayed in a 21 x 33 grid, with each patch identified as rangeland (which I assumed was bobwhite habitat) or cropland, water, or urban area (which I assumed was not bobwhite habitat) based on land cover data from Cottle County, Texas, USA (USGS-NLCD). I arbitrarily grouped sets of adjacent patches into individual properties (ranches) such that resulting mosaic of properties resembled the general configuration of real properties with regard to their sizes and shapes. Cottle County was representative of the overall composition and land use of the Rolling Plains, and had available data on local bobwhite demographic parameters. To represent differences in bobwhite habitat quality among rangeland patches due to local differences in conditions such as soil type and vegetation structure, I initialized each simulation by assigning each rangeland patch a habitat quality index ($0 \leq HQI \leq 1$) drawn randomly from a uniform distribution. I assigned non-rangeland patches a HQI of zero. I then assigned an initial density of bobwhites (BWD;

individuals/km^2) to each patch based on its HQI (BWD = 147 * HQI; 1.47 bobwhites/ha is considered a relatively high density (Leopold 1931). Note that bobwhite density is a patch attribute; bobwhites are not represented as individual entities.

System dynamics occur during each of 3 seasons (time steps) per year representing: (1) pre-breeding dispersal (approximately March through May), (2) hatching and brood rearing (approximately June–September), and (3) hunting (approximately October–February; Fig. A2-6). During pre-breeding dispersal, BWD in each patch was decreased by 40% via dispersal to adjacent patches, with dispersal equally distributed among the 8 adjacent patches (i.e., BWD was increased by an equal amount in each of the adjacent patches). Dispersal rates range between roughly 10 and 40% of the bobwhites dispersing ≥1 km from hatch location (Duck 1943, Baumgartner 1944, Madison 1998, Taylor et al. 1999, Liu et al. 2002, Townsend et al. 2003, Terhune et al. 2010). During hatching and brood rearing, BWD in each patch was increased by an amount equal to R * BWD * DD, where R represents per capita recruitment (R = 7 * HQI) and DD represents a density-dependent reduction in per capita recruitment to the population (DD = 1 - 0.00038386 * BWD, for BWD < 2605). I assumed a per capita recruitment of 7 juveniles per adult when HQI = 1 based on long-term data collected within the study area (C. Ruthven, TPWD, personal communication). During hunting, BWD in each patch is reduced by 0 to 70% depending on the harvest scenario being simulated (described below). I assumed that hunting mortality is additive to non-harvest mortality. During all 3 seasons, BWD is reduced in each patch by an amount equal to 0.33065 * M * BWD, where M represents per capita non-harvest mortality (M = 1 – 0.3

* HQI). I assumed an annual non-harvest mortality of 70% (≈33% reduction during each season) when HQI = 1 (Guthery 2002).

Harvest Experiments

I explored the effects of assuming spatially heterogeneous versus homogeneous harvest on estimates of BWD and range (number of 1-km^2 patches with >1 bird) by simulating mean, landscape-level harvest rates ranging from 10 to 70%, in 10% increments. I simulated heterogeneous harvest rates by assigning to each property a harvest rate selected randomly from a uniform distribution ranging from 10% above to 10% below the corresponding homogeneous harvest rate, and assigned that rate to each of the habitat patches within the property (i.e., harvest rates varied among properties, but not among patches within properties). Before initiating each simulation representing heterogeneous harvest, I calculated the mean landscape-level harvest rate to ensure that it was approximately equal (± 3%) to the corresponding homogeneous rate. I ran 1,000, 100-year replicate stochastic simulations of each scenario and recorded BWD and range at the end of each simulation. I analyzed differences in final BWD and range between homogenous and comparable heterogeneous scenarios at each harvest level using paired-sample *t*-tests (Zar 2010). Normal probability plots indicated that bobwhite range and density were distributed approximately normally. I conducted all statistical analyses in JMP 11.0.0 (SAS 2013).

Sensitivity Analysis

I analyzed the sensitivity of model predictions of BWD and range to changes in my representation of dispersal, per capita recruitment, and non-harvest mortality by re-running 3 replicate stochastic simulations of each of the harvest experiments described above with the following changes. I assessed the sensitivity to changes in dispersal by decreasing dispersal from 40% (baseline value) to 10% in 10% increments in both the absence of harvest, and in various scenarios relating to per capita recruitment and non-harvest mortality. I assessed the sensitivity to changes in my representation of per capita recruitment by decreasing the value of this parameter to 5 juveniles/adult when HQI = 1 to represent a relatively "worse" scenario (Table A1-5). I also conducted a separate sensitivity analysis increasing the value of this parameter to 9 juveniles/adult when HQI = 1 to represent a relatively better scenario (Table A1-5). I assessed the sensitivity to changes in my representation of annual non-harvest mortality by increasing the value of this parameter to 0.8 when HQI = 1 to represent a relatively "worse" scenario (Table A1-5). I also conducted a separate sensitivity analysis decreasing the value of this parameter to 0.6 when HQI = 1 to represent a relatively better scenario (Table A1-5). In addition to changes from baseline values, I also assessed the sensitivity to changes in the functional relationship of per capita recruitment and non-harvest mortality by conducting replicate stochastic simulations under square and square-root relationships, in addition to the baseline linear scenario. For a full graphic representation of these relationships, see figs. A2-7A–7F. For each of the 3 sensitivity analyses, I visually assessed differences in final

BWD and range between homogenous and comparable heterogeneous scenarios at each harvest level from boxplots of final BWD and range.

Results

Harvest Experiments

Simulated BWD and range were significantly different ($df = 99$, $P < 0.05$) under spatially homogeneous versus spatially heterogeneous harvest scenarios up to the 40% harvest level (Table A1-6), with lower BWDs and smaller ranges sustained under the heterogeneous harvest scenarios (Fig. A2-8A). Under both homogeneous and heterogeneous harvest, bobwhite populations were extirpated by the 50% harvest level. There was relatively little change in range under either homogeneous or heterogeneous harvest at levels <40% (Fig. A2-8B). At the 40% harvest level, there was a sharp decline in both BWD and range under both homogeneous and heterogeneous harvest, and above the 40% harvest level bobwhites were functionally extirpated from the landscape.

Sensitivity Analysis

Under all functional relationships, bobwhites were extirpated from the model landscape at lower harvest rates in relatively worse scenarios than under baseline, and at higher harvest rates under relatively better scenarios. Although the magnitude of differences in BWD and range varied slightly, the relationship of most heterogeneous and comparable homogeneous harvest levels to one another remained constant under linear (Figs. A2-10A and 10B; A2-11A and 11B), square (Figs. A2-10C, 10D, and 10E; A2-11C, 11D,

and 11E), and square root (Figs. A2-10F, 10G, and 10H; A2-11F, 11G, and 11H) functional relationships across scenarios.

Decreasing dispersal from 40% to 10% had no practically significant effect on simulated BWD or range at T_{end} (Figs. A2-9A, 9B) in unharvested populations. Increasing dispersal altered the magnitude of difference between BWD and range under homogeneous and heterogeneous harvest scenarios. Heterogeneous harvest produced higher BWD and range only at 40% harvest under relatively worse scenarios, where differences in dispersal rates seemed to strongly influence this effect (Fig. A2-10H).

Although these differences provide useful alternatives, I determined that there was no practically significant difference in the relationship of BWD and range at homogeneous and heterogeneous harvest from baseline, linear scenarios in any sensitivity analysis. I chose to retain my linear, baseline model parameterization for all harvest experiment runs. Additionally, 40% dispersal appeared to produce the median difference in BWD and the most liberal results for range between homogeneous and comparable heterogeneous harvest, so I decided to retain this rate for harvest.

Discussion

Despite coordinated harvest among properties to remove the same percent of the total bobwhites on the landscape during heterogeneous harvest simulations, BWD and range were lower than at comparable homogeneous harvest rates (Figs. A2-8A and A2-8B). Thus, it appears that estimating the effects of harvest on bobwhite populations under the assumption that harvest is applied homogeneously across the landscape may lead to overestimation of sustainable harvest levels. This has several implications for the future

harvest of bobwhites and other declining, exploited galliforms. Such sustained-percentage harvest may result in harvest mortality levels much higher than expected in the absence of coordinated, landscape-scale harvest management strategies that consider spatial heterogeneity in bobwhite subpopulations. Although Roseberry and Klimstra (1984) advocated sustained-percentage harvest as a solution to avoid bobwhite overharvest, there are problems with this approach. First, sustainable percentage harvest, as conceptualized in the context of maximum sustained yield (Caughley 1977), was rarely known for bobwhites. Second, individual property managers set harvest rates across their properties based on their experience and harvest goals, but rarely coordinate harvest management with adjacent properties (Conner 2007). As a result, remnant bobwhite subpopulations exist within a mosaic landscape of harvest and habitat management strategies. Thus, I assert that sustained-percentage harvest rates are ultimately unsustainable for bobwhites when they do not consider spatial aspects of the species' ecology and hunting practices vis-à-vis local extinction thresholds, as hypothesized by Bascompte and Sole (1996) and McCullough (1996) for limited dispersal, *r*-selected species in fragmented habitats.

This study was a first step in understanding landscape-scale bobwhite population responses to spatial heterogeneity in harvest, as suggested by Roseberry (1991). In my model, harvest under heterogeneous scenarios produced lower BWD and range than under comparable homogeneous scenarios, even though the differences were small (Figs. A2-8A and 8B). Spatially heterogeneous harvest may influence population dynamics of other declining, exploited galliform species to a greater extent than

suggested by earlier studies, due to a disconnect between harvest management and spatial aspects of species' ecology (Akçakaya et al. 2004, Beissinger et al. 2006, Blomberg et al. 2012). I therefore suggest that new harvest strategies must be implemented to account for the effects of heterogeneous harvest in bobwhites and other declining, exploited galliforms. In order to provide such strategies, however, wildlife managers must first develop a clear understanding of the spatial aspects of harvest. To date, wildlife regulators have enacted moratoriums on hunting for declining galliforms in some areas (Johnson and Braun 1999, The Scottish Government 2001, Silvy and Hagen 2004). Although closing the hunting season undoubtedly removes 1 source of mortality, it does not address what many consider the primary cause of the decline of numerous exploited galliforms worldwide: changing land use and habitat fragmentation (Rands 1992, IUCN 2013). As human-induced land changes continue, it is likely that many galliform populations will no longer be viable.

The harvest of many galliforms is an economically important activity (Conner 2007, McGowan et al. 2009). Thus, closing hunting seasons may adversely affect human cultures and economies based on galliform harvest, thereby de-incentivizing habitat management beneficial to galliforms. In the absence of the economic benefits of galliform harvest, further habitat fragmentation or loss may ensue. It is therefore critical that wildlife managers and regulators provide strategies that allow for the future of galliform harvest while protecting these species from localized extinctions due to overharvest. It may be possible for individual properties (or cooperatives of properties) to maintain viable bobwhite subpopulations (sensu Guthery et al. 2000) within their

borders, even under high harvest pressure, given sufficiently large area, such as during my 40% heterogeneous harvest scenarios in various sensitivity analyses (e.g. Figs. A2-10C and A2-11H). One possible explanation is that such properties functioning as harvest reserves by supporting high bobwhite abundance under comparatively lower harvest rates during these heterogeneous harvest scenarios. These harvest reserves could protect isolated subpopulations in the face of broad-scale land use change. Similar designs were employed in Texas, USA during the early 20th century for bobwhites (Lehmann 1984), and recently proposed by Willebrand and Hörnell-Willebrand (2001) for willow ptarmigan (*Lagopus lagopus*) in Norway. The logical extension of my results would be research investigating the potential of spatial or temporal harvest reserves to mitigate the effects of heterogeneously distributed harvest. I recommend using this study as a reference to construct harvest field experiments that manipulate various harvest management strategies to determine which, if any, may be sustainable for declining, exploited galliform species in the long-term.

CHAPTER IV

INFLUENCES OF TEMPERATURE AND RELATIVE HUMIDITY ON USABLE NESTING HABITAT FOR NORTHERN BOBWHITES AT THE WESTERN PERIPHERY OF THEIR RANGE

Synopsis

Ecologists have long recognized the influence of weather on abundance and range extent of animal species. The northern bobwhite (*Colinus virginianus*; hereafter bobwhite) is an excellent model for exploring the ability of specific microclimates to serve as refuge against severe weather conditions. I conducted a mensurative field experiment in the Rolling Plains of Texas, a semi-arid ecosystem on the southwestern periphery of bobwhite range, to determine whether native bunch grasses apparently suitable for bobwhite nesting could sufficiently reduce ambient temperature below harmful levels for eggs. I compared temperature and relative humidity at 126 paired locations (63 random and 63 nesting), each with 2 sensors (~10 cm and ~60 cm above ground) throughout the nesting season. Mean temperatures were 36.81°C (*SE* = 0.0683) and 35.99°C (*SE* = 0.0645) at nest height in random and nesting cover locations, respectively, and 32.78°C (*SE* = 0.0549) and 32.99°C (*SE* = 0.0551), at ambient height in nesting and random locations, respectively. Mean relative humidity was 34.53% (*SE* = 0.112), and 33.35% (*SE* = 0.116) in nesting cover, and random locations at nest height, respectively, and 36.22% (*SE* = 0.101), and 35.75% (*SE* = 0.099) in nesting, and random locations at ambient height, respectively. Based on my results, bobwhite nesting cover provides

adequate thermal refuge in the Rolling Plains by maintaining cooler, moister microclimates than surrounding random points. Given that bobwhite eggs would otherwise experience potentially lethal temperatures without these thermal refugia, nesting vegetation is a critical component of bobwhite habitat in semi-arid regions. Many contemporary land uses, however, degrade or destroy bunch grasses and thus decrease habitat availability through time for bobwhites. Conservationists working with bobwhites and other species that require bunch grasses in semiarid regions should develop land management strategies that maximize the availability of these thermal refugia across space and time.

Introduction

Ecologists have long recognized the influence of weather on abundance and range extent of animal species. For example, Birch (1957) found that extreme temperature (hot or cold) or precipitation (wet or dry periods) influenced population dynamics of diverse animal species worldwide. In arid and semi-arid regions, heat often constrains the inhabitable area of a landscape (Cameron 1981, Salzman 1982, Parker and Gillingham 1990, Carey 2009, Hansen 2009), and animals often seek refuge in more cool and/or moist microclimates (e.g., caves, dense vegetation) (Dawson et al. 2000, Sheldon et al. 2010, Sinervo et al. 2010). Thus, these refugia can extend the range of species to areas that would be otherwise uninhabitable.

The northern bobwhite (*Colinus virginianus*; hereafter bobwhite) is an excellent model for exploring the ability of specific microclimates to serve as refuge against severe weather conditions. The abundance and range of this New World quail species

are strongly influenced by various aspects of weather. Quail biologists have long recognized that extreme cold (Robinson and Baker 1955), prolonged ice and snow coverage (Roseberry 1964, Klimstra and Roseberry 1975), flooding (Stoddard 1931, Lehmann 1984), and extreme heat (Johnson and Guthery 1988, Forrester et al. 1998, Guthery et al. 2005b) limit bobwhite production and survival. In semi-arid ecosystems on the western edge of the bobwhite's range (Hernández and Peterson 2007), extreme heat can render available habitat inhospitable, cause asynchronous incubation, kill adults, and stunt or kill embryos, thereby severely limiting bobwhite production (Guthery et al. 2001, Reyna 2010, Reyna and Burggren 2012). Bobwhites nest in vegetation (i.e., native bunch grasses) that likely maintains cooler microclimates through the interaction of sun-shading and evaporative cooling (Johnson and Guthery 1988, Guthery et al. 2005*b*, Hernández and Peterson 2007, Rader et al. 2007). As a result, these vegetative structures may be essential components of bobwhite habitat. Drought and livestock grazing, however, often limit the availability of such vegetation in semi-arid regions, thereby reducing potential bobwhite production (Bridges et al. 2001, Guthery et al. 2002). Thus, lack of thermal refugia due to drought, heavy livestock grazing, or other land uses that consumes or degrades essential vegetation, reduces available habit and therefore lowers the landscape carrying capacity below levels required for viable bobwhite subpopulations (Forrester et al. 1998, Guthery 1999, Guthery et al. 2000). Although the necessity of thermal refugia for bobwhites at the semi-arid extent of their range is well known, the ability of nesting structures to maintain thermally-suitable microclimates is not well-documented.

Earlier research provided ancillary evidence regarding the importance of thermal refugia for bobwhites in semi-arid ecosystems. Earlier studies found that broad scale weather phenomena that influence the production of nesting vegetation (e.g., precipitation, temperature) could explain a large proportion of the variability in bobwhite abundance among years (Lehmann 1984, Bridges et al. 2001, Guthery et al. 2002, Lusk et al. 2002). Although such inferences are valuable, these data were collected at a scale too broad to capture the influence of weather-related phenomena relevant to individual bobwhites. Laboratory studies quantified the relationship between heat stress, reduced immunocompetence of adults, developmental plasticity, and embryo death (Dabbert et al. 1997, Reyna 2010, Reyna and Burggren 2012). These studies demonstrated the physiological effects of severe heat loads on individual bobwhites at various life history stages, but could not address heat loads experienced by bobwhites *in situ*. A few field studies attempted to quantify heat experienced by wild bobwhites, but were limited by small spatial and temporal extent, and did not address nesting structures (e.g., Forrester et al. 1998, Guthery et al. 2001, Guthery et al. 2005b).

I conducted an intensive mensurative field experiment (Hurlbert 1984) in the Rolling Plains of Texas (Gould 1969), a semi-arid ecosystem on the western edge of the range of the bobwhite, to test the hypothesis that native bunch grass vegetation apparently suitable for bobwhite nesting can act as thermal refugia for bobwhites. Specifically, I monitored temperature and relative humidity within vegetation suitable for bobwhite nesting cover and at random points to determine whether temperature and relative humidity differed at daily heat maxima during bobwhite nesting season (roughly

1 May–31 September; Hernández and Peterson 2007) (1) at 2 heights: that experienced by bobwhites, and an estimate of ambient temperature, (2) 2 locations: within vegetation suitable for bobwhite nesting, and paired, random points of various cover types, and (3) through the nesting season (1 May–31 September). I discuss my results with respect to the limits of bobwhite nesting cover as thermal refugia, and extend the implications to other species that use similar microclimates to avoid harmful heat stress. I end with effects of weather-related stress on species, particularly those experiencing rapid changes in habitat due to land use change.

Means and Methods

Study Area

The Rolling Plains of Texas (Gould 1969) is a semi-arid physiographic region in northwestern Texas that historically supported large bobwhite subpopulations that are now declining in abundance. Topography is characterized by flat to gentle rolling plains intersected by streams that flow in an east to southeasterly direction; elevation ranges from 215 to 950 m. Soils vary from coarse sands to tightly packed clays, with substantial fine scale variability in soil type. Annual precipitation increases in an easterly direction, from roughly 550 mm to nearly 760 mm. May and September are the wettest months, with a summer dry period. This region forms part of the southern end of the Great Plains. Plant communities historically were dominated by mid or tall bunch grass species, including little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), sand bluestem (*Andropogon hallii)*, Indian grass (*Sorghastrum nutans*), and

sideoats grama (*Bouteloua curtipendula*). Riparian areas supported woody plant communities that included oaks (*Quercus spp.),* eastern cottonwood (*Populus delitoides*), elms (*Ulmus spp.*), and junipers (*Juniperus spp.*). Extensive woody plant encroachment due to overgrazing and/or fire suppression has resulted in reduction of grass-dominated range sites. Honey mesquite (*Prosopis glandulosa*) is a common invader throughout the Rolling Plains, while shinnery oak (*Quercus havardii*) and sand sage (*Artemisia filifolia*) invade primarily on sandy soils. As a result, rangeland comprised of mixed native grass-herbaceous vegetation with interspersed shrubs characterizes much of the land cover. Although livestock grazing operations dominate land use across this region as a whole, many areas have been converted to cropland (USDA-NASS 2007).

I conducted my study on 6 ranches dispersed across the Rolling Plains, which range in size from roughly 1,600 to 78,200 ha. These ranches capture much of the variation in land conditions (i.e., geology, soil type, vegetation, and topography) experienced by bobwhites in the Rolling Plains ecoregion. All 6 ranches were managed for a combination of livestock grazing and fee hunting. Livestock grazing intensity varied between ranches, but was consistent within ranches. All ranches experienced drier conditions during my study than normal due to an ongoing drought. Further, all ranches were somewhat drier during 2012 than 2013, and 3 sites experienced wildfires during 2011 that removed all vegetation on ≥60% of those sites.

Data Collection

I collected temperature and relative humidity data using a spatially nested (multi-scalar) sampling design along sampling transects on 6 ranches within the Rolling Plains ecoregion of Texas (Gould 1969). On each ranch I established sampling points, with a minimum separation of 1 km between points. I established only 9 and 10 sample points on 2 ranches due to transect length constraints, and 11 sample points on the other 4. I used model DS1923 hygrochron iButton temperature/humidity sensors (hereafter sensors;Dallas Semiconductor 2011) mounted inside the open cavity on the underside of yellow, Red Snap'r® screw-on type electric fence post insulators (Fig. A2-12) on a 1-m piece of steel rebar. The fence post insulators protected sensors against direct insolation, weather (i.e., hail, flood), and animal damage. I padded between insulator and sensor with foam inserts, and secured sensors to insulators with a white cable tie. Mounted sensors were aligned toward the west. Four sensors at each sample point collected hourly temperature and relative humidity data at 2 heights (10 cm and 60 cm) in 2 locations (random point and nesting cover). The 10-cm height corresponded with the height of a bobwhite nest, and a height of 60 cm was used as an estimate of ambient temperature. For the purposes of this study, I defined nesting cover as the center of the clump of native bunch grass suitable for bobwhite nesting nearest to the random point (Rader et al. 2007). I moved nesting sensors before each nesting season if senescence and degradation of the previous year's nesting cover had occurred. Random points were placed 25 m from the sampling transect every 1 km of transect travelled, alternating left or right. Points were checked to ensure they were no closer together than every 1 km. These

transects representatively traversed every vegetation cover type on each ranch. Random points were located in various cover types, but only 3% occurred in vegetation (i.e., woody plants, grasses) that may have provided some effect on *in situ* temperature and relative humidity. Sensors collected temperature and relative humidity hourly for 2 years (January 2012–January 2014). I downloaded data from sensors every 4 months using the Thermodata Viewer Software (Thermodata Corporation 2011). During download, I removed sensors from mounts, inspected mounts for damage, replaced damaged mounts, and replaced foam inserts and cable ties. Raw data were later reformatted, and imported into a relational database. I ranked relative bobwhite habitat quality of each sampling point from excellent to poor based on ocular estimates of percent ground cover, and grass and forb availability and diversity from photo points taken each May and September (Fig. A2-13).

Analyses

I compared temperature and relative humidity between cover types and sensor heights using repeated-measures, split-block analyses of variance (ANOVA) with 1 within-factor (time as month) and 2 between-factors (sensor height and cover type). This method accounts for lack of independence when repeated observations were obtained from the same experimental units (Tzilkowski and Storm 1993, von Ende 2001, Zar 2010). Environmental heterogeneity among ranches was controlled by blocking (Zar 2010, Gotelli and Ellison 2012). I examined differences in temperature and relative humidity during daily heat maxima (i.e., 1300–1500 hours) in bobwhite nesting season (1 May to 31 September): (1) between random and nesting locations, (2) between

ambient and nesting heights, and (3) across months. Critical assumptions were assessed prior to hypothesis testing. All analyses were conducted in JMP Pro 11.0.0 (SAS 2013), and I considered $p < 0.05$ significant.

Plots of normality and residual variance indicated that temperature and relative humidity data were approximately normally distributed and homoscedastic. Mauchley's test for sphericity (circularity; Mauchly 1940) revealed a lack of sphericity in the temperature variance-covariance matrix ($W = 0.3823$; $X^2 = 27{,}697.107$, $P < 0.001$) and in the relative humidity variance-covariance matrix ($W = 0.7032$; $X^2 = 10{,}142.523$, $P < 0.001$). I therefore used the more conservative Greenhouse-Geisser corrected F-test (Greenhouse and Geisser 1959, Huynh and Feldt 1970) to assess treatment effects for temperature ($\varepsilon = 0.3823$) and relative humidity ($\varepsilon = 0.7032$) data. I visually evaluated trends between treatment factors and range condition using both plots of mean temperature and relative humidity during daily heat maxima to assess the ability of nesting cover to reduce *in situ* heat below harmful levels.

Results

Temperature

When examining the effect of between-subjects factors (location, height) on temperature by month, I found a significant ($P < 0.001$) main effect between both locations and heights (Table A1-7). There was a significant ($P < 0.001$) interaction between location and height, however, which indicates that monthly temperatures at both nesting and random locations were largely dependent upon height. When considering the within-

subjects factor (time) on *in situ* temperatures, I found a significant ($P < 0.001$) main effect of month (Table A1-7). Nevertheless, the interactions of month and location, month and height, and month, location, and height were significant ($P < 0.001$), indicating that time, alone, was not the driving influence on temperature.

Mean temperature was higher at nest height in random locations ($\bar{x}$ = 36.81, *SE* = 0.0683) than at nest height in nesting cover locations ($\bar{x}$ = 35.99, SE = 0.0645). Mean temperatures at ambient height in nesting and random locations were essentially identical ($\bar{x}$ = 32.78, *SE* = 0.0549 and $\bar{x}$ = 32.99, *SE* = 0.0551, respectively). During the course of my study, 54.2% of temperature readings occurred between 0 and 40°C ($\bar{x}$ = 34.65, *SE* = 0.031), a temperature range suitable for bobwhites.

Relative Humidity

For between-subjects factors influencing mean relative humidity by month, I found a significant ($P < 0.001$) main effect between heights, but not locations (Table A1-8). The presence of a significant ($P < 0.001$) interaction between location and height, however, indicated differences between locations depended primarily on height. Although I found a significant ($P < 0.001$) main effort for the within-subjects factor (month) on relative humidity (Table A1-8), interactions among month and location, month and height, and month, height, and location were significant ($P < 0.001$), indicating that time was not the driving force in mean relative humidity. Thus, while the influence of time was statistically significant, *in situ* relative humidity is largely dependent on height, and to a lesser extent, location.

Overall, mean relative humidity was higher at nest height in nesting cover locations ($\bar{x}$ = 34.53, *SE* = 0.112) than nest height in random locations ($\bar{x}$ = 33.35, *SE* = 0.116). Similarly, ambient height in nesting locations exhibit higher mean relative humidity ($\bar{x}$ = 36.22, *SE* = 0.101) than ambient height in random locations ($\bar{x}$ = 35.75, *SE* = 0.099). During the course of my study, 80.0% percent of relative humidity readings occurred between 19% and 100% relative humidity ($\bar{x}$ = 34.96, *SE* = 0.054).

Monthly and Daily Trends

Monthly means plots indicate divergent mean temperature and relative humidity across months of the nesting season primarily based on height (Figs. A2-14 and A2-15). Trends for both temperature and relative humidity were similar, regardless of height or location, although the magnitude of the differences was based primarily on height. Ambient heights exhibited similar trends, and experienced coolest mean temperatures and lowest mean relative humidity throughout the day. Differences in temperatures and relative humidity between height/location combinations were smallest at the beginning and end of the nesting season.

Nest height in nesting locations experienced cooler temperatures and higher relative humidity than nest height in random locations during daily heat maxima. Nevertheless, both nesting and random locations at nest height appeared to maintain harmful and/or lethal temperatures throughout much of the nesting season during daily heat maxima whether viewed by month (Figs. A2-14 and A2-15) or day (Figs. A2-16 and A2-17). Differences between nesting and random locations at nest height appeared biologically insignificant across all ranches (Figs. A2-14–A2-17). Trends in temperature

and relative humidity at nest height in nesting and random locations on 3ranches that represent excellent, moderate, and poor range conditions, however, revealed that temperatures were below harmful levels (~40° C) for longer in nesting cover on ranches with better range conditions (Figs. A2-18 and A2-19).

Discussion

Based on my results, I suggest that bobwhite nesting cover can provide thermal refuge in the Rolling Plains on the southwestern periphery of the species range by maintaining a cooler, moister microclimate than surrounding random points. *In situ* temperature and relative humidity differed significantly primarily as a result of cover type, and to a lesser extent height, during my study. Cooler microclimates in nesting cover result from the insulatory capacity of bunch grasses to resist temperature fluctuation *vis-à-vis* thermal mass and evaporative cooling, thereby moderating grass temperature at ground height, as well as the air space above it (Barbour et al. 1999). A portion of the temperatures recorded during my study not only meets, but also exceed the thermal thresholds for bobwhites documented in laboratory studies (Dabbert et al. 1997, Reyna 2010, Reyna and Burggren 2012). Thus, I conclude that thermal refugia are necessary for bobwhites, particularly eggs pre-incubation and adults during incubation, to avoid heat stress that characterizes the semi-arid portion of their range, as suggested by Forrester et al. (1998), Guthery et al. (2001), and Guthery et al. (2005b).

Given that bobwhite eggs would experience potentially lethal heat stress without nesting cover suitable for thermal refugia, it is logical that such vegetation is a critical component of bobwhite habitat in the semi-arid portion of the species' range. Because

bobwhites reproduce during summer, exhibit limited-dispersal ability, and are a relatively *r*-selected species (Roseberry and Klimstra 1984, Hernández and Peterson 2007, Lohr et al. 2011), it is critical that nesting cover suitable for thermal refugia be present across broad spatial extents and through time to maximize bobwhite production (Guthery 1999). I suggest that the greatest contribution of nesting cover as thermal refuge for bobwhite eggs is during temperature maxima at the peak of bobwhite nesting, when availability of thermally suitable bobwhite nesting habitat is most tightly constrained.

Ultimately, variability in weather and land use defines the thermal suitability of a landscape for bobwhites. Previous studies demonstrated the strong influence of weather (i.e. precipitation and temperature) on bobwhite abundance in the semi-arid portions of the bobwhite's range (Lehmann 1984, Bridges et al. 2001, Guthery et al. 2002, Lusk et al. 2002). Fluctuations in precipitation, including frequent, extended droughts, limits the production and quality of nesting cover in this physiographic region (Lehmann 1946, Lusk et al. 2006, Sands et al. 2012). Thus, any land use that further reduces the availability of thermal refugia during the nesting season (e.g., excessive livestock grazing, broad scale tillage) also would reduce bobwhite landscape carrying capacity. During the course of this study, the ability of nesting cover to reduce experienced heat below harmful levels appeared to be related to relative range conditions (Figs. A2-17 and A2-18). I suggest that the additional indirect insolation from bare ground around nesting cover is largely responsible for this effect. Whether the result of livestock grazing practices, the historic drought affecting the Rolling Plains during my study, or

both, some study sites provided nesting cover that would have been thermally suitable for laying, incubation, and hatching quail for a longer portion of the nesting season than others. Although bobwhites existed historically under diverse agricultural land uses across their range (small farms to large ranches; Leopold 1931, Jackson 1969), the extensification (Morgan-Davies et al. 2014) and/or intensification of land use threatens bobwhites. Over the last several decades, traditional agricultural systems have been replaced in the Rolling Plains by extensive "clean farming" cultivation and excessive cattle grazing (Peterson et al. 2002, USDA-NASS 2007, Wilkins et al. 2009). These land uses often degrade or destroy bobwhite nesting cover, thereby lowering bobwhite carrying capacity by severely constraining habitat availability through space and time, particularly thermally-suitable nesting cover (Guthery et al. 2005b).

Where bobwhites persist in semi-arid ecosystems, land uses that maximize agricultural production often produce landscapes that exist at thermal limits for bobwhite habitat. Thus, these habitats expand and contract with weather variability, but are further constrained by anthropogenic landscape changes that increase temperatures by exposing more bare ground or degrading existing nesting cover (Foley et al. 2005, Favreau et al. 2009). Although such "on-the-knife's-edge" land management may not appear to destroy bobwhite habitat during normal rainfall years, weather extremes (i.e., extended drought, abnormally high temperature) may raise *in situ* temperatures in bobwhite nesting cover above threshold lethal limits (Brown 1978), such as during the drought conditions experienced throughout this study. Thus, areas that might otherwise fulfill habitat requirements are no longer bobwhite habitat due to "brinkmanship" management (sensu

MacNab 1985). Quail biologists recognize such habitat loss, fragmentation, and degradation as key contributors to long term declines in bobwhite abundance and range (Williams et al. 2004). As landscape fragmentation increases, these same factors likely disrupt metapopulation dynamics, and induce localized extinction events (Bascompte and Sole 1996). In order to decelerate or reverse declining bobwhite abundance and range extent in semi-arid ecosystems, land use practices should be modified to provide all aspects of bobwhite habitat in perpetuity (i.e., continual through both space and time;(Guthery 1999). These land use practices must be coordinated across broad expanses, maintain adequate thermal refugia throughout the year, and operate reflexively to changing weather conditions (Peterson 2007).

Management Implications

Bunch grass nesting cover is an important component of habitat for bobwhites in the Rolling Plains of Texas because it provides thermal refuge from harmful heat for both adults and eggs. For those concerned with the survival of this species, habitat management provisions that provide adequate thermal refugia are essential. The influence of thermal stress on survival and reproduction requires species to seek thermal refuge from severe temperature, whether bobwhites, other birds (Salzman 1982, Goldstein 1984, Thomas 1984), deer (Parker and Gillingham 1990), rats (Hendersen and Graham 1979), lizards (Monasterio et al. 2009, Sinervo et al. 2010), or fishes (McDaniel et al. 1991). As anthropogenic land use changes continue to accelerate, it is likely that habitat fragmentation will increase, thereby reducing available thermal refugia and effectively constraining available habitat for a number of species. Thus, changes in land

use that exceed lethal thermal limitations may play an important role in the recent range wide decline in many species' abundance.

The interaction of weather and habitat fragmentation may affect the availability and quality of thermal refugia to mitigate heat stress by increasing temperatures *in situ* (Opdam 1991, Delattre et al. 2013). For species whose range is characterized by potentially harmful weather (e.g., extreme heat or cold, drought or flood), the loss of such refugia will likely disrupt metapopulation dynamics at various scales(Vitousek et al. 1997, Monasterio et al. 2009), thereby increasing the chance of local or range-wide extinction events (Mantyka-pringle et al. 2012). Therefore, it is critical to begin modifying land use practices to minimize their impact on thermal aspects of species' habitats. In order to decelerate or reverse this trend, land use practices must be developed (or redeveloped) (Bignal and McCracken 1996, Webb 1998, Bignal and McCracken 2000) that maximize thermal refugia throughout the year. Such practices must identify critical habitat requirements in both space and time to maximize conservation potential for species that require thermal refugia.

CHAPTER V

CONCLUSIONS

In the preceding studies, I investigated various influences of harvest and environmental factors on northern bobwhites in the Rolling Plains of Texas. In chapter II, I examined what aspects of bobwhite abundance and hunter effort most strongly predicted total quail harvest in Texas. I considered relative indices of abundance calculated from TPWD roadside surveys, as well as total hunter-days and total hunters that represented a measure of hunter effort. In chapter III, I further examined whether the spatial distribution of harvest pressure (homogeneous versus heterogeneous) influenced mean bobwhite density and range in a simulation model parameterized to represent the Rolling Plains. Finally, in chapter IV, I tested whether elements of nesting habitat could ameliorate lethal heat stress on bobwhite eggs *in situ*, a prominent environmental factor that influences bobwhite production in the Rolling Plains.

My work produced several insights into the influences of both harvest and habitat management on bobwhites. First, I determined that the factors that influence total bobwhite harvest in the various regions of Texas are incongruent with statewide trends (Tables A1-1 and A1-3). Thus, assumptions about harvest regulation based on statewide trends are likely not applicable to all regions. In the Rolling Plains, both the abundance of bobwhites as well as the number of days hunters spend afield most strongly explains harvest. Because a measure of hunter effort factors so strongly, it is unlikely that current regulations can limit bobwhite harvest at small enough scales to prevent localized

overharvest in the Rolling Plains. In turn, such overharvest could lead to broad scale declines in bobwhite abundance and range, or accelerate ongoing declines. Second, in my simulation of the influence of heterogeneously applied harvest pressure at the landscape scale, I determined that such harvest tends to result in lower landscape-level bobwhite density and range than under homogeneously applied harvest (Figs. A2-8A and A2-8B). Because harvest in the real world is applied heterogeneously and previously published sustainable harvest estimates relied on the assumption of homogeneously applied harvest pressure, it is likely that those land managers attempting to harvest a sustained percent harvest may, in fact, be harvesting a larger proportion of the bobwhites on their property than they estimate. Furthermore, under either homogeneous or heterogeneously applied harvest pressure, local extinction thresholds remained similar.

Finally, my investigation of the ability of bunch grasses used as nesting cover to adequately provide thermal refuge for bobwhite eggs revealed that such structures do maintain lower temperatures during heat maxima. Further, this ability to ameliorate heat stress was strongest during the late summer, when such nesting structures are at the peak of their growth cycle (Fig. A2-14). Interestingly, the results of my study indicated that overall range condition surrounding each clump of nesting cover was influential in dictating the amount of time during the nesting reason that such nesting cover was thermally suitable for bobwhite eggs (Fig. A2-18).

The results of my studies translate into practical recommendations for those who manage both harvest and habitat for bobwhites on individual properties in the Rolling Plains of Texas. Harvest management on such properties should be conducted at the

smallest practical scale (i.e., pasture scale), as suggested by Williams et al. (2004). Because quail hunter days seems to be among the most important factors influencing total harvest across the Rolling Plains, management at the pasture scale likely will limit the pressure applied in order to prevent localized overharvest. Further, other research indicates that late-season hunting may have a stronger influence on bobwhite population trends than early-season hunting (Guthery et al. 2004b). Thus, both the spatial and temporal aspects of bobwhite harvest must be carefully managed to avoid localized overharvest. Considering a somewhat broader scale, individual property managers should attempt to coordinate harvest efforts with neighboring properties in order to remain above the landscape level extinction threshold. Regionally, any efforts to regulate quail harvest should address hunter behaviors that drive harvest in that region.

Because bobwhites are a relatively *r*-selected species, ensuring maximum annual net recruitment is the first concern of those interested in maintaining viable bobwhite populations. Thus, habitat management should focus on the maximization of nesting structure interspersion and quality during the height of bobwhite nesting season in the Rolling Plains. This often coincides with the peak of bunch grass growth, as well as annual heat maxima. To achieve this goal, livestock grazing must be carefully managed to leave adequate structure to bunch grass clumps in order for these nesting substrates to retain the capacity to serve as a thermal refuge. Further, the habitat surrounding suitable bunch grass clumps should be maintained at a relatively high range condition to ensure that indirect insolation does not cause bunch grass clumps to exceed harmful levels for

bobwhite eggs. This may be generally accomplished by carefully managing livestock grazing, especially during times of drought.

In conclusion, the intersection of harvest and habitat management for bobwhites addresses the same issue: moderation of resource use. Most bobwhite harvest occurs in conjunction with livestock grazing operations. As such, both grazing and harvest must be moderated in order to ensure healthy bobwhite subpopulations and vegetative resources to provide for continued production of both huntable bobwhites and livestock. Only the individual property manager has adequate incentive to carefully steward natural resources to this outcome, given that careful management is essential for the continued economic viability of their property. Indeed, it is difficult to imagine a land manager who would intentionally reduce their long-term earning potential. Rather, it is possible that a lack of both clear management recommendations, as well management reflexive with changing weather conditions (i.e., drought) that often characterizes this region, are likely the source of resource over-use that leads to declining bobwhite abundance and range. It is my hope the results of my work will help inform future management decisions in the Rolling Plains of Texas, as well as encourage other natural resource scientists to further investigate the issues I herein addressed.

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APPENDIX 1

TABLES

Table A1-1. Candidate regression models using quail abundance (QA), total quail hunters (QH), and total quail hunter-days (QHD) to account for statewide annual total harvest of northern bobwhites in Texas from log-transformed harvest and abundance survey data 1978–2012 using AICc model selection.

Model	K[a]	-2lnL	AICc[b]	Δ_i[c]	ω_i[d]	$\omega_{1/}\omega_i$	R^2
QA + QHD	3	-29.56	-22.56	0.0	0.839	1	0.969
QA + QH	3	-26.10	-19.10	3.5	0.149	5.651	0.965
QHD	2	-17.54	-13.06	9.5	0.007	115.833	0.952
QH	2	-16.65	-12.17	10.4	0.005	180.594	0.950
QA	2	16.09	20.57	43.1	0.000	2,328,872,309	0.830

[a] Number of estimable parameters, including the intercept.
[b] Akaike's information criterion corrected for small sample size.
[c] ΔAICc.
[d] Akaike weight.

Table A1-2. Candidate regression models using quail abundance (QA), total quail hunters (QH), and total quail hunter-days (QHD) to account for statewide annual total harvest of scaled quail in Texas from log-transformed harvest and abundance survey data from the years 1978–2012 using AICc model selection.

Model	K^a	-2lnL	AICc[b]	Δ_i[c]	ω_i[d]	ω_1/ω_i	R^2
QA + QH	3	2.10	9.10	0.0	0.983	1	0.915
QA + QHD + (QA x	4	8.36	18.09				0.894
QHD)				9.0	0.011	89.873	
QH	2	15.97	20.45	11.3	0.003	291.081	0.859
QA + QHD	3	13.69	20.69	11.6	0.003	328.504	0.871
QHD	2	24.95	29.43	20.3	0.000	25,936.331	0.865
QA	2	39.61	44.09	35.0	0.000	39,673,737.390	0.672

[a] Number of estimable parameters, including the intercept.
[b] Akaike's information criterion corrected for small sample size.
[c] ΔAIC.
[d] Akaike weight.

Table A1-3. Set of plausible ($\Sigma\ W_i \geq 0.95$) candidate regression models using quail abundance (QA), total quail hunters (QH), and total quail hunter-days (QHD) to account for annual total harvest of bobwhite in 6 ecological regions of Texas from log-transformed harvest and abundance survey data from the years 1978–2012 using AICc model selection.

Ecological Region	Model	K^a	-2lnL	AICc[b]	Δ_i[c]	ω_i[d]	ω_1/ω_i	R^2
High Plains	QA + QH	3	9.34	16.60	0.0	0.468	1	0.891
	QH	2	12.29	16.89	0.3	0.406	1.155	0.877
	QA + QH + (QA x QH)	4	9.37	19.60	3.0	0.105	4.462	0.892
Rolling Plains	QA + QHD	3	-22.01	-15.01	0.0	0.609	1	0.962
	QA + QHD + (QA x QHD)	4	-22.21	-12.47	2.5	0.171	3.565	0.963
	QA + QH	3	-18.70	-11.71	3.3	0.117	5.228	0.957
Edwards Plateau	QHD	2	-6.39	-1.91	0.0	0.399	1	0.949
	QA + QH + (QA x QH)	4	-10.38	-0.65	1.3	0.213	1.879	0.957
	QH	2	-4.27	0.21	2.1	0.139	2.885	0.945
	QA + QHD	3	-6.47	0.53	2.4	0.118	3.380	0.950
	QA + QH	3	-4.94	2.06	4.0	0.055	7.252	0.947
South Texas Plains	QHD	2	-12.03	-7.55	0.0	0.659	1	0.928
	QA + QHD	3	-11.84	-4.84	2.7	0.170	3.878	0.928
	QH	2	-6.43	-1.95	5.6	0.040	16.458	0.911

Table A1-3, continued.

Ecological Region	Model	K^a	-2lnL	AICc[b]	Δ_i[c]	ω_i[d]	ω_1/ω_i	R^2
Gulf Coast Prairies	QA + QH	3	33.76	40.76	0.0	0.702	1	0.679
	QH	2	39.21	43.69	2.9	0.162	4.326	0.607
	QA + QHD + (QA x QHD)	4	35.62	45.36	4.6	0.070	10.000	0.660
	QHD	2	41.94	46.42	5.7	0.041	16.935	0.566
Cross Timbers	QA + QH + (QA x QH)	4	8.47	18.21	0.0	0.470	1	0.954
	QH	2	14.03	18.51	0.3	0.406	1.158	0.943
	QA + QH	3	14.04	21.04	2.8	0.114	4.115	0.943

[a] Number of estimable parameters, including the intercept.
[b] Akaike's information criterion corrected for small sample size.
Table 3, continued.
[c] ΔAIC.
[d] Akaike weight.

Table A1-4. Set of plausible ($\Sigma\ W_i \geq 0.95$) candidate regression models using quail abundance (QA), total quail hunters (QH), and total quail hunter-days (QHD) to account for annual total harvest of scaled quail in 5 ecological regions of Texas from log-transformed harvest and abundance survey data from the years 1978– 2012 using AICc model selection.

Ecological Region	Model	K^a	-2lnL	AICc[b]	Δ_i[c]	ω_i[d]	ω_1/ω_i	R^2
High Plains	QA + QH	3	31.32	39.04	0.0	0.800	1	0.796
	QA + QH + (QA x QH)	4	31.84	42.91	3.9	0.115	6.953	0.797
	QA + QHD	3	36.20	43.92	4.9	0.070	11.499	0.733
Rolling Plains	QH	2	36.66	41.20	0.0	0.562	1	0.826
	QA + QH	3	35.11	42.25	1.1	0.332	1.694	0.790
	QA + QH + (QA x QH)	4	35.39	45.39	4.2	0.069	8.117	0.790
Edwards Plateau[e]	QA + QH	3	24.89	31.89	0.0	0.496	1	0.853
	QH	2	28.84	33.31	1.4	0.243	2.040	0.835
South Texas Plains[e]	QH	2	-11.33	-6.85	0.0	0.671	1	0.960
	QA + QH	3	-11.52	-4.52	2.3	0.209	3.207	0.960
Trans-Pecos[e]	QA + QHD	3	34.84	41.84	0.0	0.563	1	0.763
	QHD	2	39.47	43.95	2.1	0.195	2.880	0.718

Table A1-4, continued

[a] Number of estimable parameters, including the intercept.
[b] Akaike's information criterion corrected for small sample size.
[c] ΔAIC.
[d] Akaike weight.
[e] I did not report 95% confidence sets for these regions because the model that included the interaction term was not sufficiently different from the model without the interaction term.

Table A1-5. Equations for parameterizing northern bobwhite annual hatch per adult and non-harvest mortality under better, baseline, and worst scenarios with square root, linear, and square relationships with habitat quality (HQI).

Scenario	Parameter	Functional relationship		
		Square root	Linear	Square
Better	Hatch	= 9 * √HQI	= (9 * HQI) + 0	= 9 * HQI^2
	Non-Harvest Mortality	= 1 – (0.4 * √HQI)	= (-0.4 * HQI) + 1	= 1 - (0.4 * (HQI^2))
Baseline	Hatch	= 7 * √HQI	= (7 * HQI) + 0	= 7 * HQI^2
	Non-Harvest Mortality	= 1 – (0.3 * √HQI)	= (-0.3 * HQI) + 1	= 1 - (0.3 * (HQI^2))
Worse	Hatch	= 5 * √HQI	= (5 * HQI) + 0	= 5* HQI^2
	Non-Harvest Mortality	= 1 – (0.2 * √HQI)	= (-0.2 * HQI) + 1	= 1 - (0.2 * (HQI^2))

Table A1-6. Mean BWDs and ranges (at T_{End}) simulated under heterogeneous and comparable homogeneous harvest scenarios. Test statistics (paired-sample *t*-tests (Zar 2010)) were significant ($P < 0.05$) for all comparisons except BWD and range at 40 and 50% harvest. Asterisks indicate inadequate data for comparisons due to extirpation of all bobwhites during simulation.

Harvest rate (%)	BWD			Range		
	Homogeneous	Heterogeneous	Test statistic	Homogeneous	Heterogeneous	Test statistic
10	12.69	11.2387	$t = -6.687$	662	644	$t = -22.045$
20	9.00	8.24	$t = -2.217$	660	639	$t = -8.727$
30	4.99	4.29	$t = -3.30$	634	617	$t = -6.519$
40	0.67	0.83	$t = 1.666$	335	363	$t = 1.049$
50	0.00	0.00	$t = 1.234$	1.5	7.4	$t = 1.341$
60	*	*	*	*	*	*
70	*	*	*	*	*	*

Table A1-7. Results of 2 repeated measures analysis of variance (ANOVA) addressing the effects of sensor height (~10 cm and ~60 cm), sensor location (bunch grasses suitable for bobwhite nesting cover and paired random points), time (month of the nesting season), and interactions among these factors on temperature (°C) in the Rolling Plains of Texas, USA, 2012–2014.

	Factor	***F*-ratio**	***P*-value**
Between subject factors	Location	165.8683 (0.0058, 28817)	<0.0001
	Height	8.6881 (0.0003, 28817)	<0.001
	Location x Height Interaction	925.3084 (0.0321, 28817)	<0.0001
Within subject factors	Month	28,468.312 (0.615, 70899)	<0.0001
Interaction with time	Location	19.1627 (0.615, 70899)	<0.0001
	Height	100.3514 (0.615, 70899)	<0.0001
	Location x Height	299.6004 (0.615, 70899)	<0.0001

Table A1-8. Results of 2 repeated measures analysis of variance (ANOVA) addressing the effects of sensor height (~10 cm and ~60 cm), sensor location (bunch grasses suitable for bobwhite nesting cover and paired random points), time (month of the nesting season), and interactions among these factors on percent relative humidity in the Rolling Plains of Texas, USA, 2012–2014.

Factor		F-Ratio	*P*- value
Between subjects factor	Location	0.4269 (0.0001, 28817)	0.5135
	Height	20.6770 (0.0007, 28817)	<0.0001
	Location x Height Interaction	629.0051 (0.0218, 28817)	<0.0001
Within subjects factor	Month	10428.092 (0.8319, 95893)	<0.0001
Interaction with time	Location	34.3273 (0.8319, 95893)	<0.0001
	Height	27.0177 (0.8319, 95893)	<0.0001
	Location x Height	142.9113 (0.8319, 95893)	<0.0001

APPENDIX 2

FIGURES

Figure A2-1. Trends in northern bobwhite abundance (mean quail per 32-km survey route), total number of bobwhite hunters, and total bobwhite hunter-days in Texas, 1978–2012.

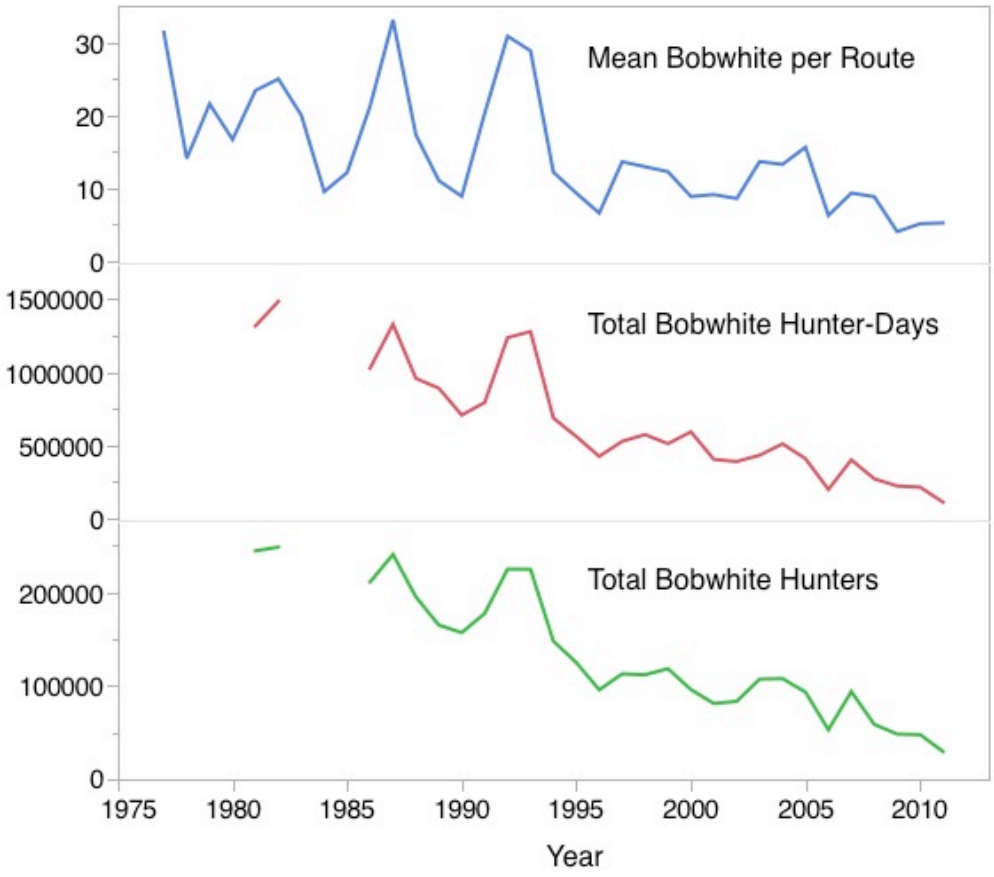


Figure A2-2. Trends in scaled quail abundance (mean quail per 32-km survey route), total number of scaled quail hunters, and total scaled quail hunter-days in Texas, 1978–2012

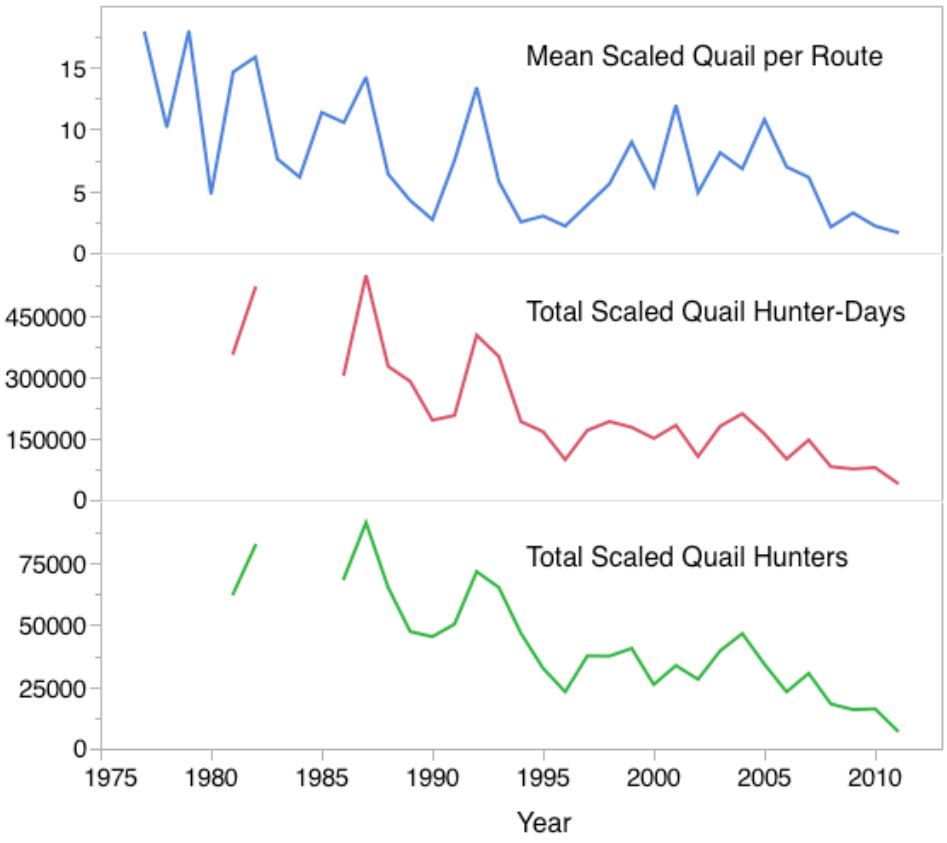


Figure A2-3. Trends in (a) northern bobwhite abundance (mean quail per 32-km survey route), (b) total number of bobwhite hunters, and (c) total bobwhite hunter-days in Texas by ecological region, 1978–2012

Figure A2-3A

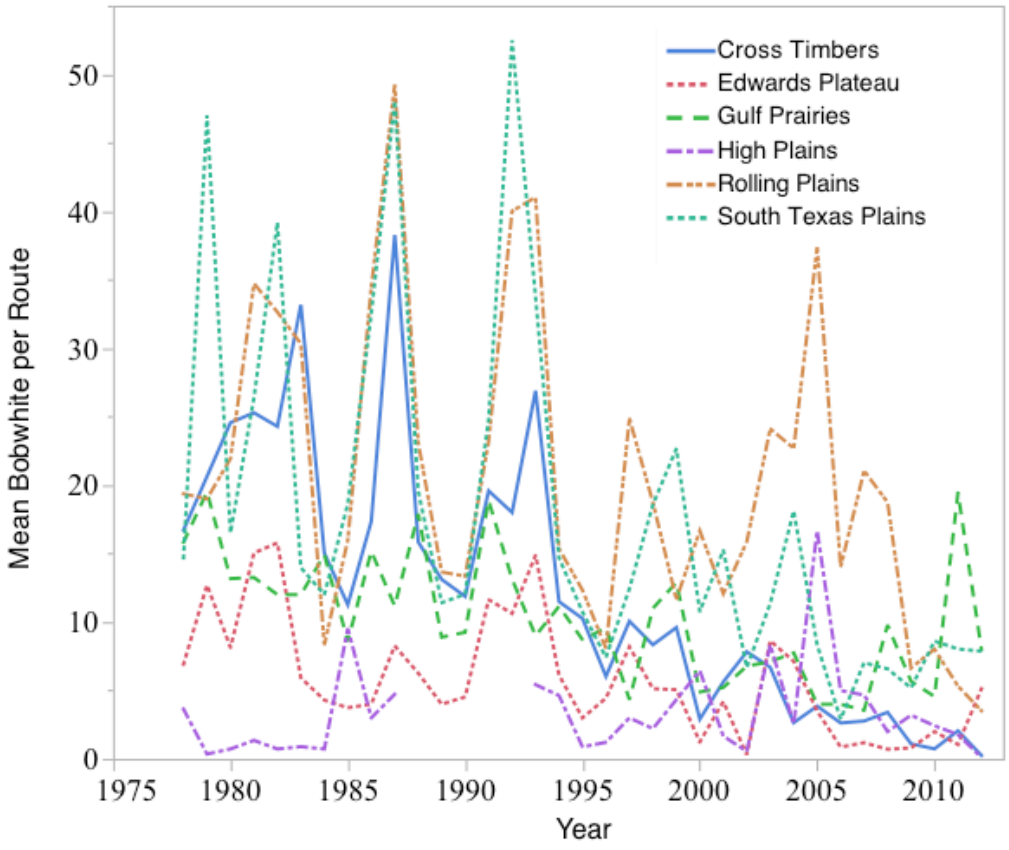


Figure A2-3B

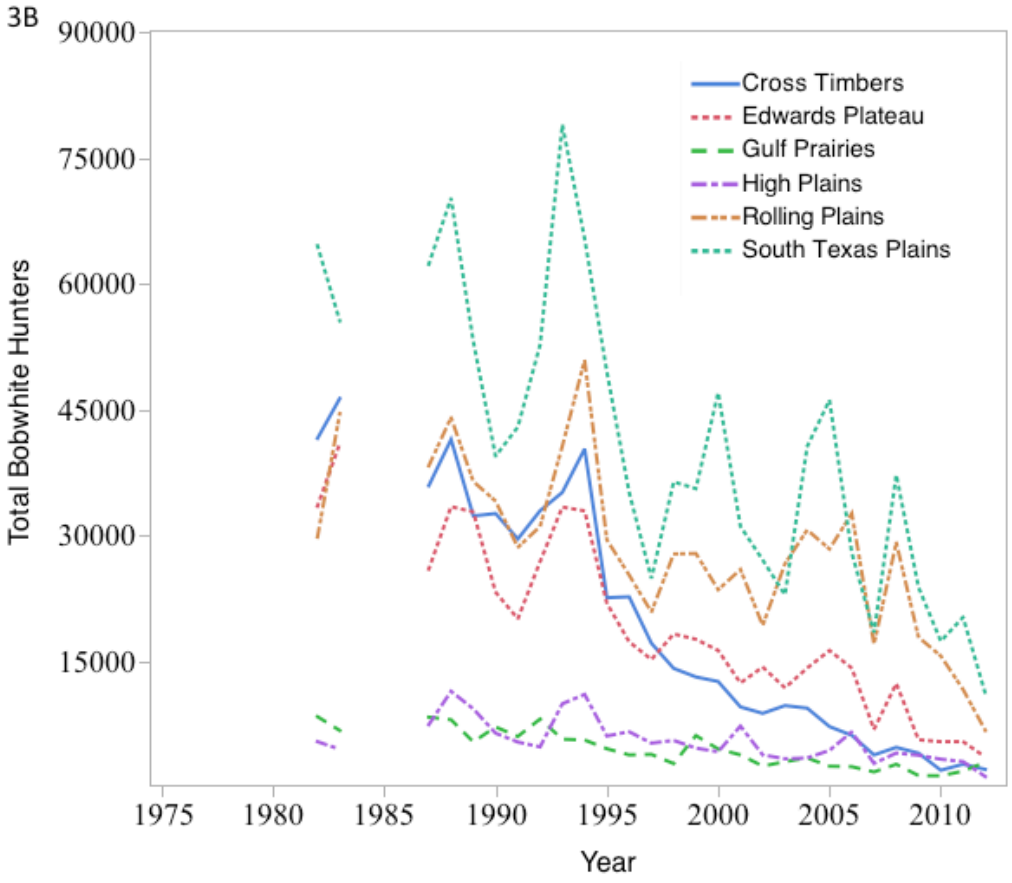

3B
90000
75000
60000
45000
30000
15000
Total Bobwhite Hunters
1975
1980
1985
1990
1995
2000
2005
2010
Year
Cross Timbers
Edwards Plateau
Gulf Prairies
High Plains
Rolling Plains
South Texas Plains

Figure A2-3C

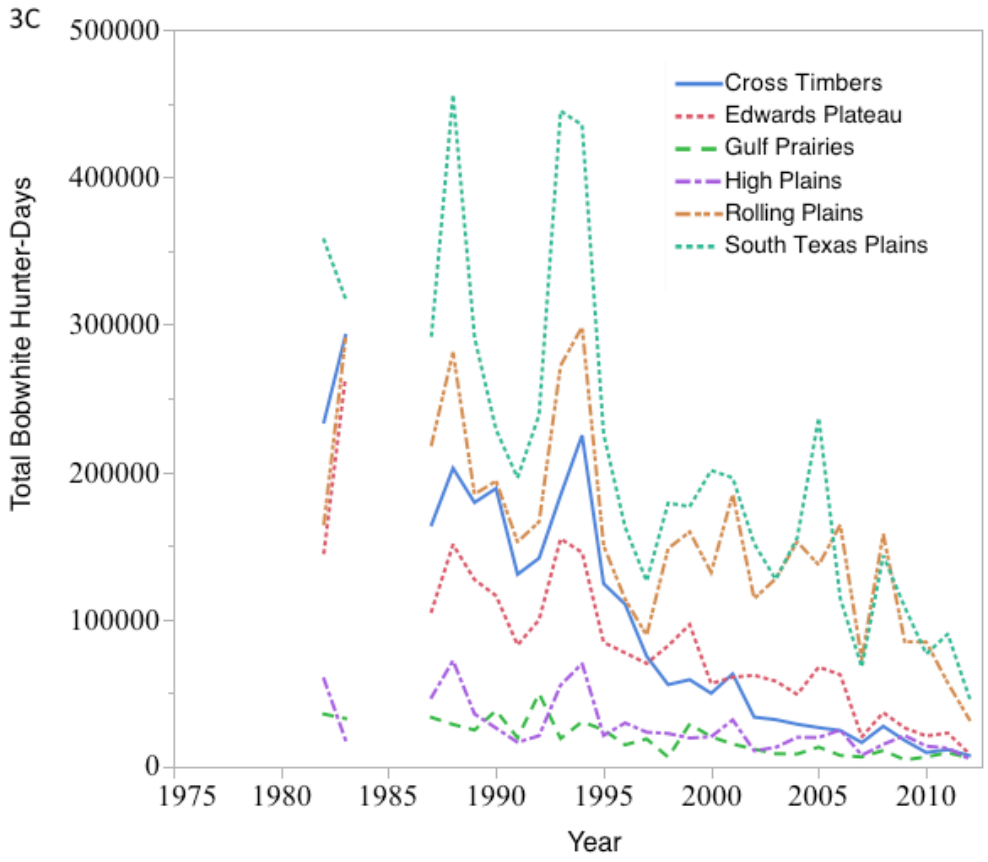

3C
Total Bobwhite Hunter-Days
500000
400000
300000
200000
100000
0
1975
1980
1985
1990
1995
2000
2005
2010
Year
Cross Timbers
Edwards Plateau
Gulf Prairies
High Plains
Rolling Plains
South Texas Plains

Figure A2-4. Trends in (a) scaled quail abundance (mean quail per 32-km survey route), (b) total number of scaled quail hunters, and (c) total scaled quail hunter-days in Texas by ecological region, 1978–2012.

Figure A2-4A

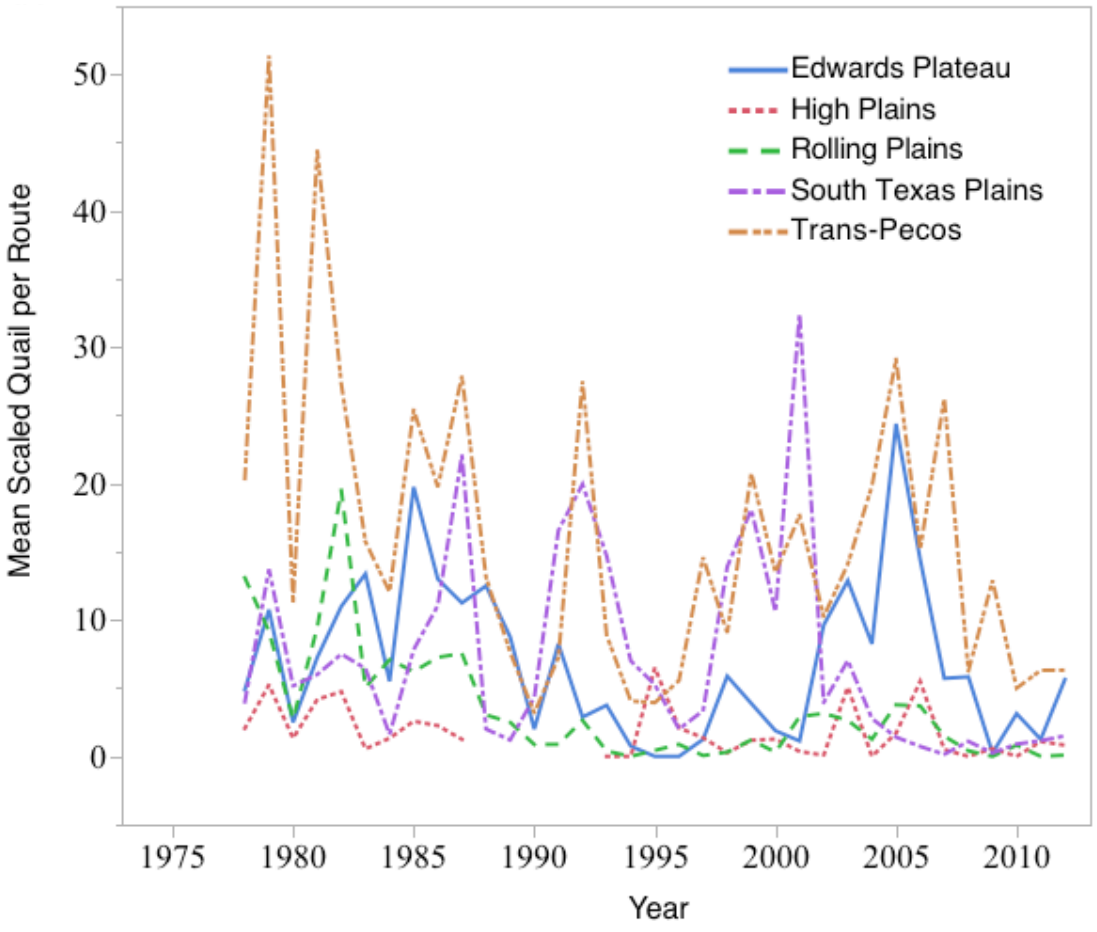


Figure A2-4B

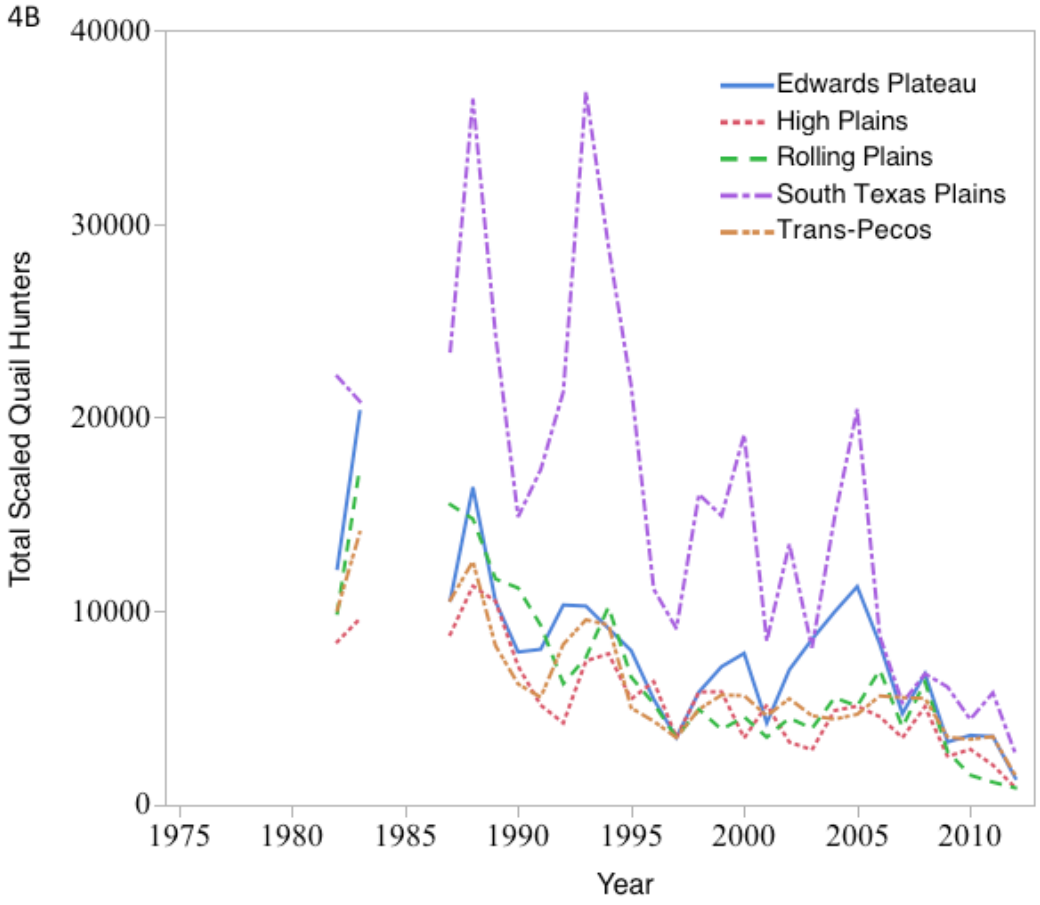

4B
40000
30000
20000
10000
0
Total Scaled Quail Hunters
1975
1980
1985
1990
1995
2000
2005
2010
Year
Edwards Plateau
High Plains
Rolling Plains
South Texas Plains
Trans-Pecos

Figure A2-4C

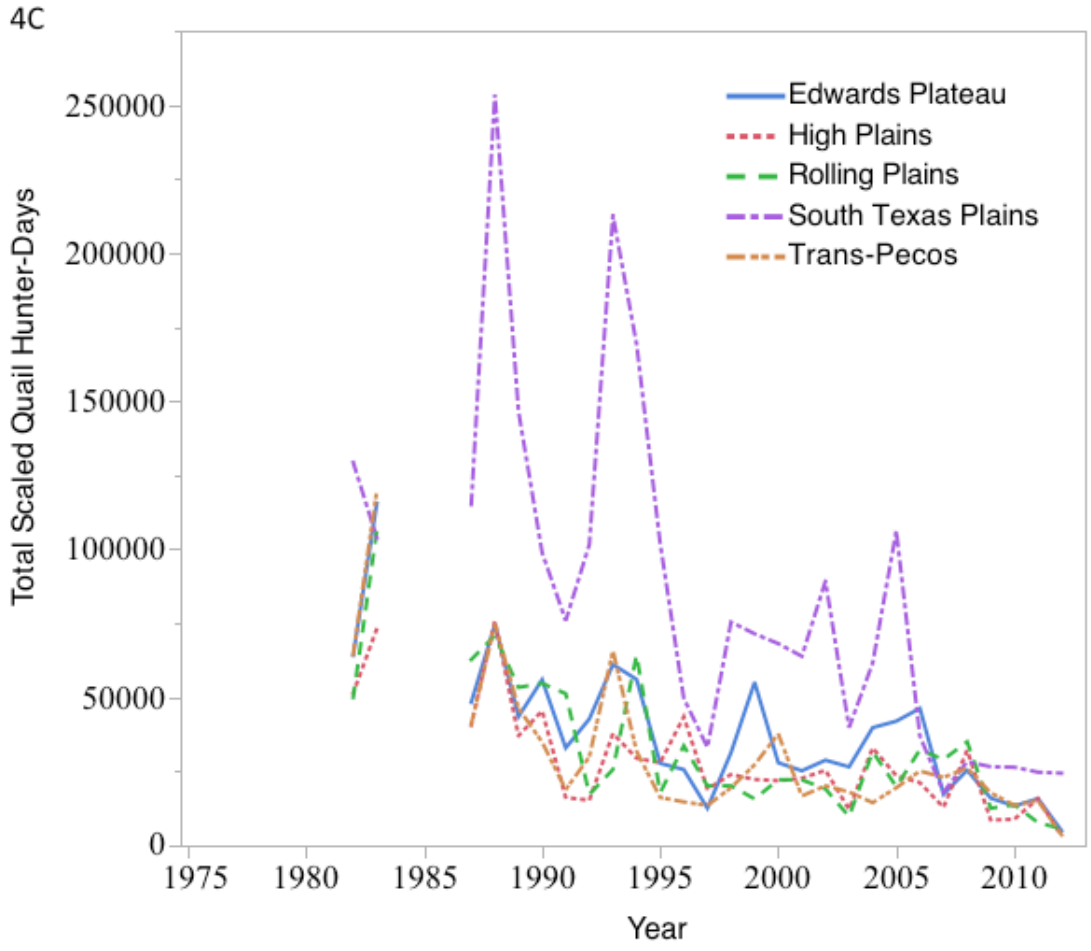
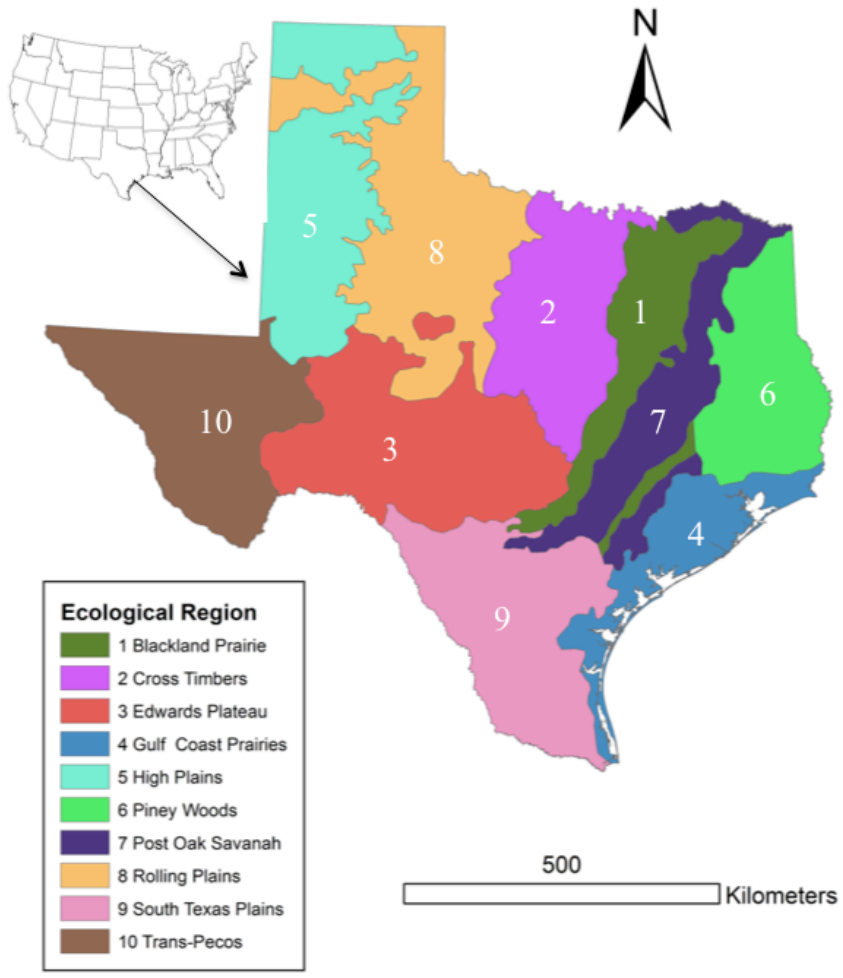

4C
Total Scaled Quail Hunter-Days
250000
200000
150000
100000
50000
0
1975
1980
1985
1990
1995
2000
2005
2010
Year
Edwards Plateau
High Plains
Rolling Plains
South Texas Plains
Trans-Pecos

Figure A2-5. Texas ecological regions (Gould 1969).



Source: Gould, F. W. 1969. Texas plants: a checklist and ecological summary. – Texas Agricultural Experimental Station, Texas A&M University System.

Figure A2-6. Location, conceptual spatial structure, and functional relationships represented in the model system of northern bobwhite harvest on rangelands in northwestern Texas, USA, superimposed onto simulated individual properties, that simulates the hatch, dispersal to adjacent patches, and non-harvest and harvest mortality of northern bobwhites subpopulations. A habitat quality index drives hatch and non-harvest mortality rates.

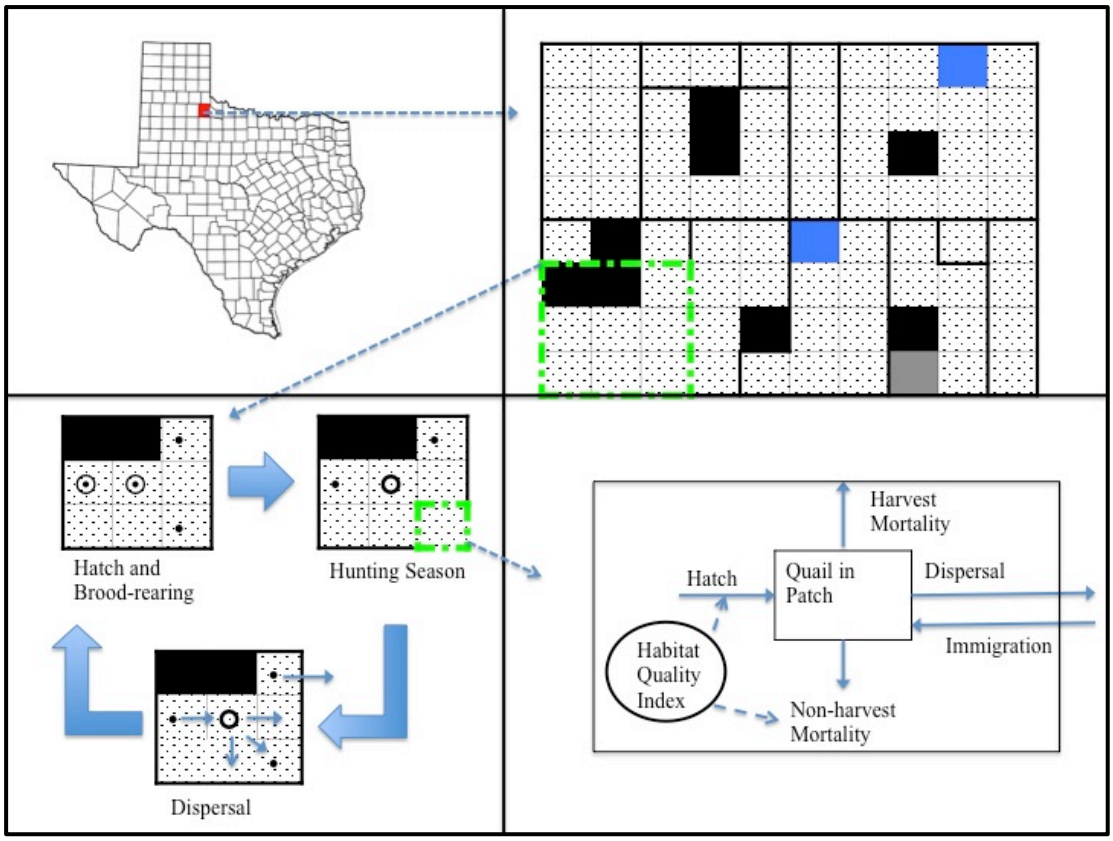


Figure A2-7. Functional relationships between northern bobwhite recruitment (juveniles/adult) and annual non-harvest mortality (%), and HQI according to linear, square root, and square formulas under baseline (7A, 7B), relatively better (7C, 7D), and relatively worse (7E, 7F) conditions.

Figure A2-7A

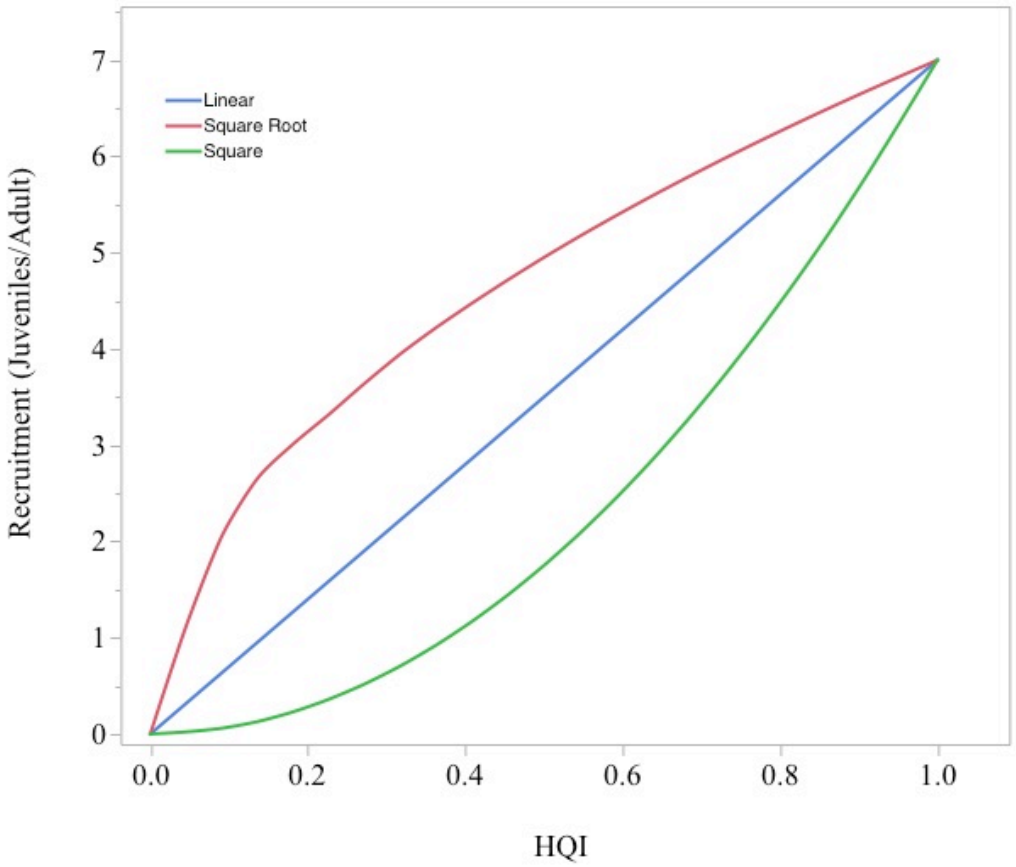


Figure A2-7B

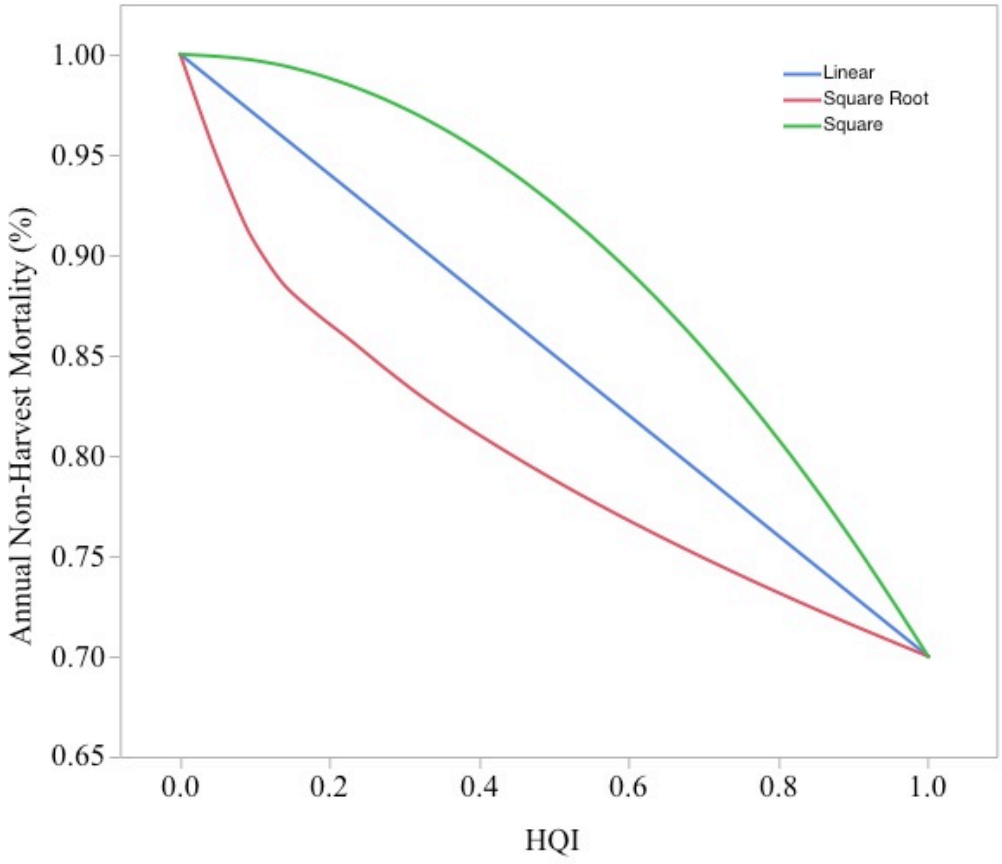

Linear
Square Root
Square
Annual Non-Harvest Mortality (%)
1.00
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.0
0.2
0.4
0.6
0.8
1.0
HQI

Figure A2-7C

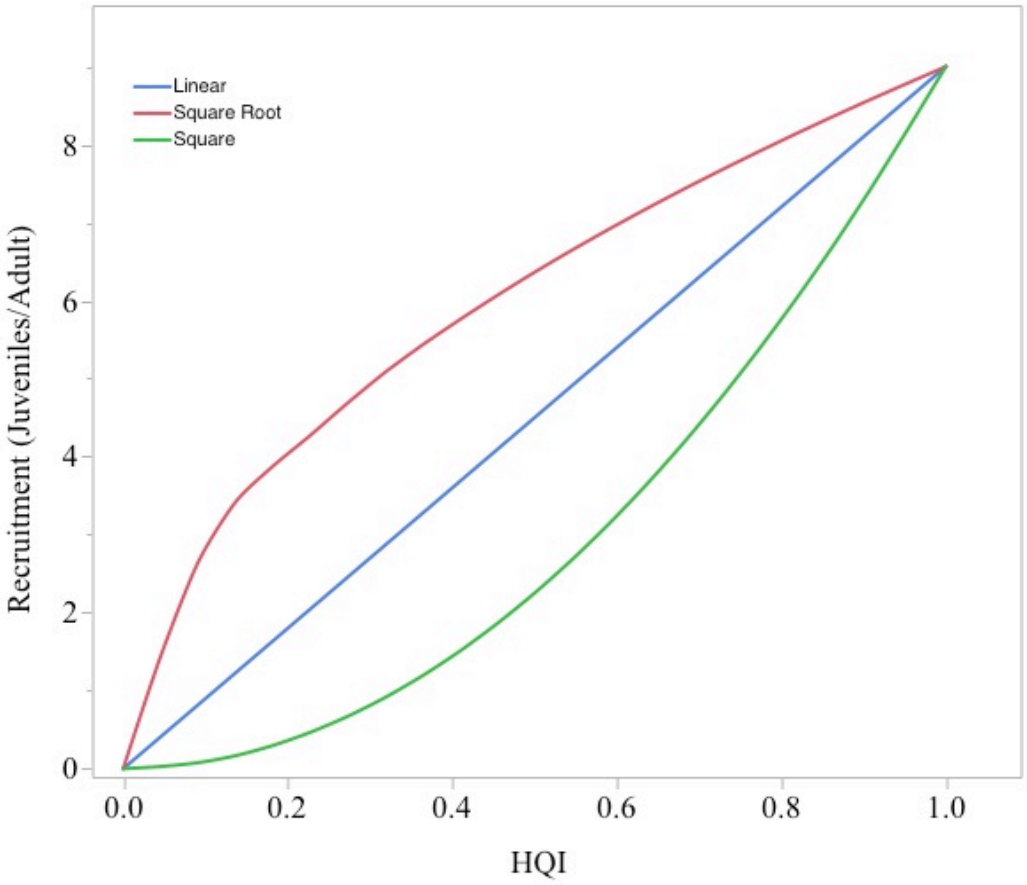

Linear
Square Root
Square
Recruitment (Juveniles/Adult)
0
2
4
6
8
0.0
0.2
0.4
0.6
0.8
1.0
HQI

Figure A2-7D

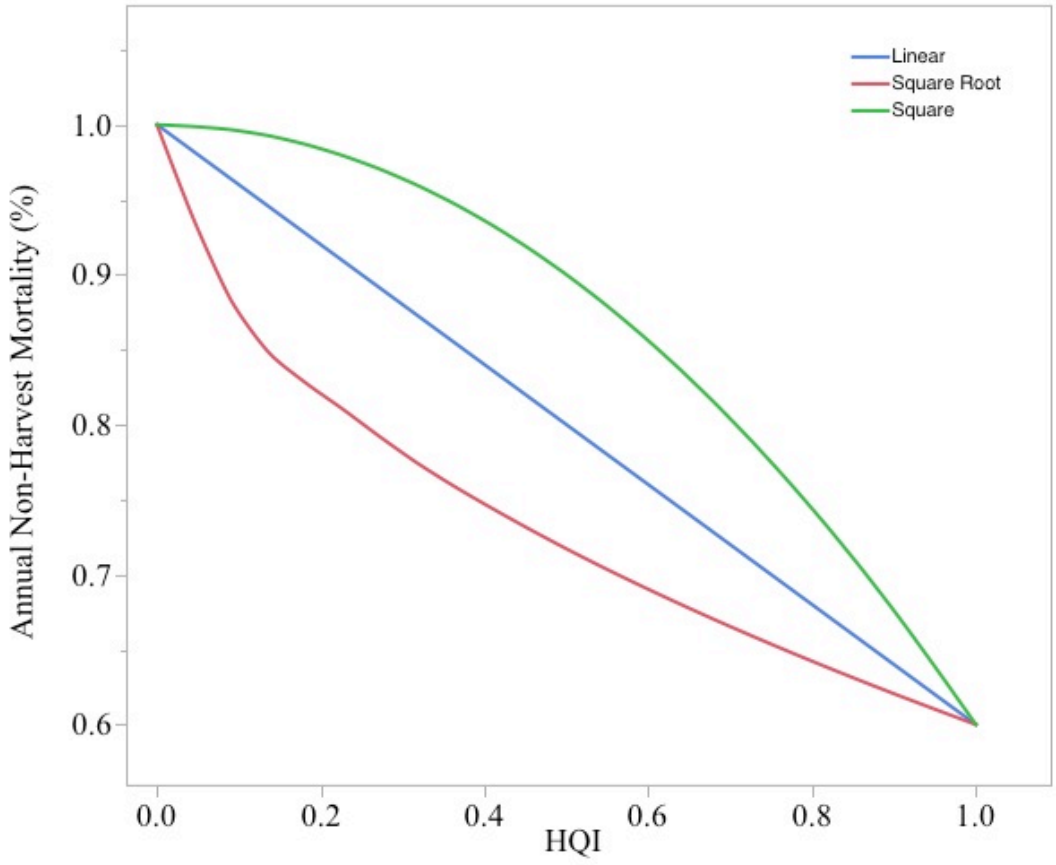

Linear
Square Root
Square
Annual Non-Harvest Mortality (%)
1.0
0.9
0.8
0.7
0.6
0.0
0.2
0.4
0.6
0.8
1.0
HQI

Figure A2-7E

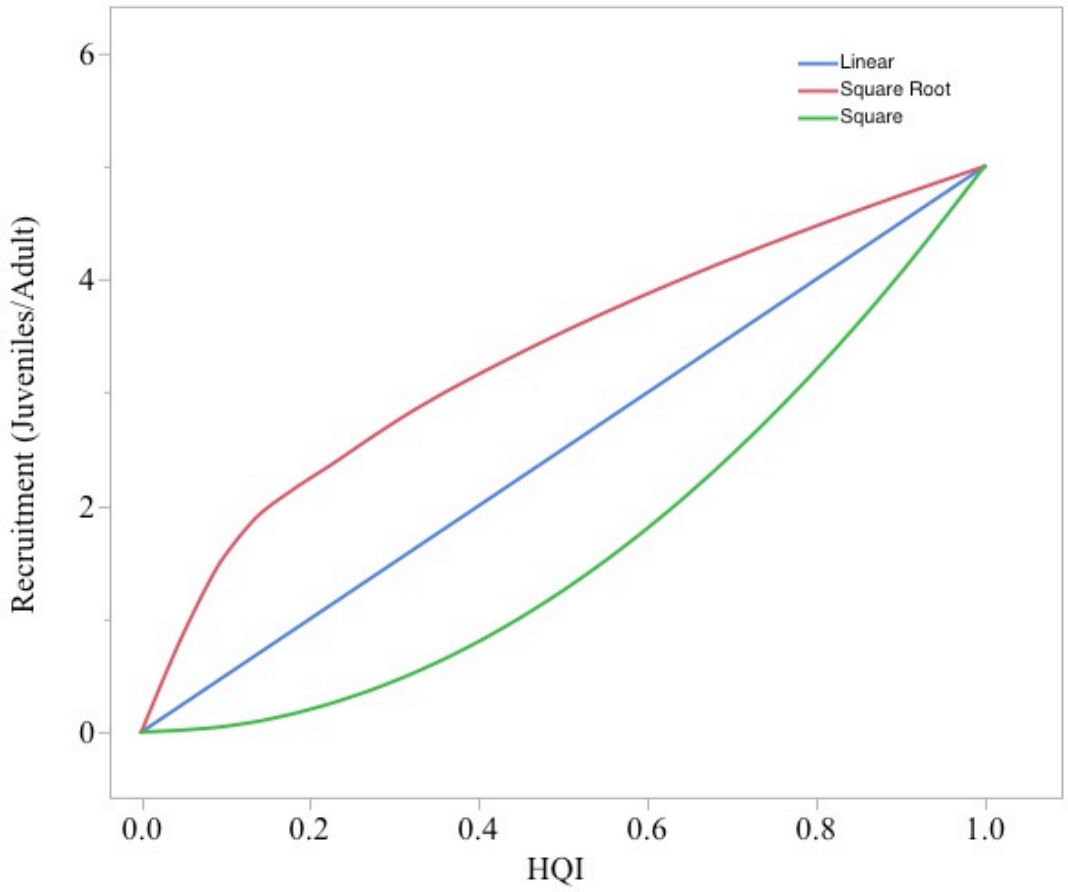

Linear
Square Root
Square
Recruitment (Juveniles/Adult)
6
4
2
0
0.0
0.2
0.4
0.6
0.8
1.0
HQI

Figure A2-7F

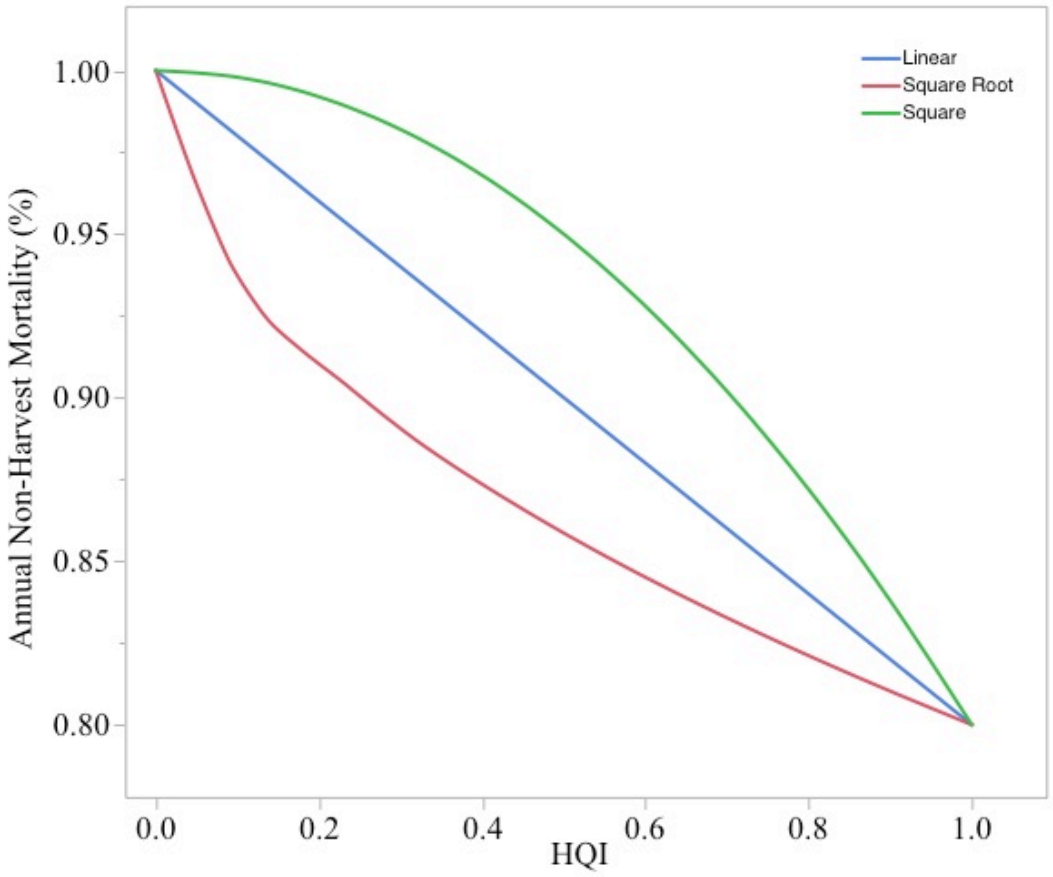

Linear
Square Root
Square
1.00
0.95
0.90
0.85
0.80
Annual Non-Harvest Mortality (%)
0.0
0.2
0.4
0.6
0.8
1.0
HQI

Figure A2-8. BWD (A) and range (B) at t_{end} under the indicated harvest scenarios with 10% variation above and below mean harvest rates in spatially heterogeneous harvest levels. Boxes represent means (+/-1SD) and whiskers represent maximums and minimums of 100 Monte Carlo simulations.

Figure A2-8A

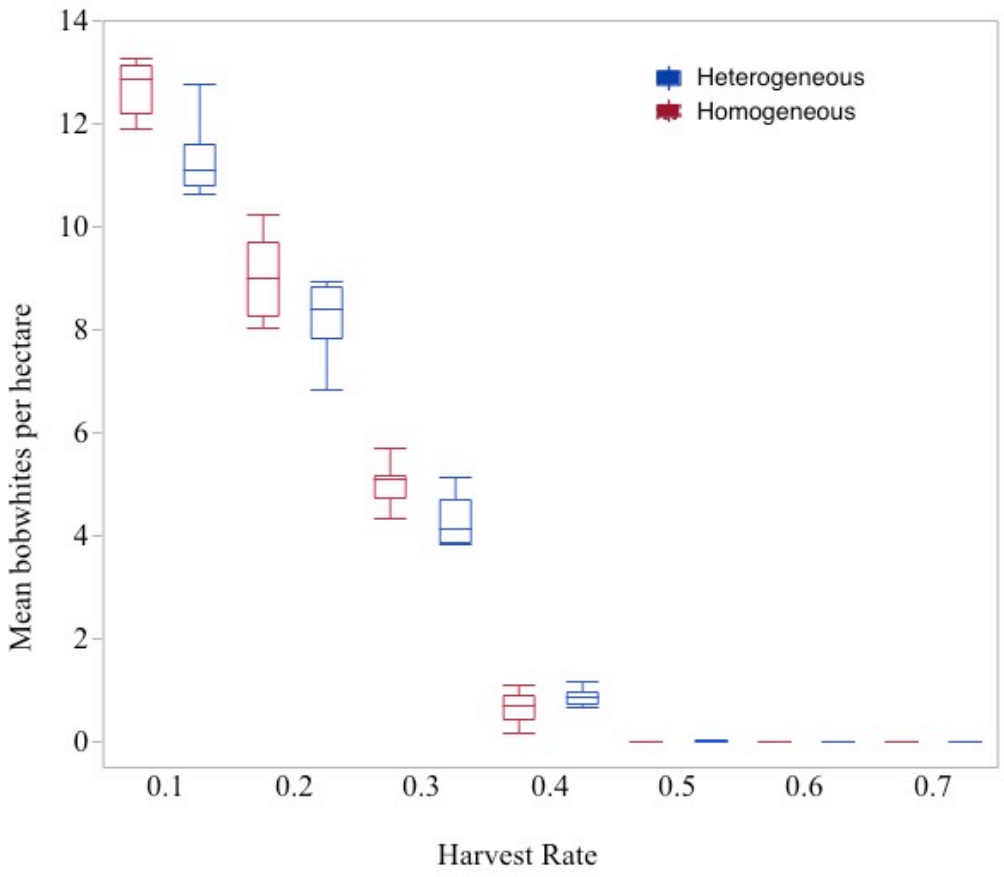


Figure A2-8B.

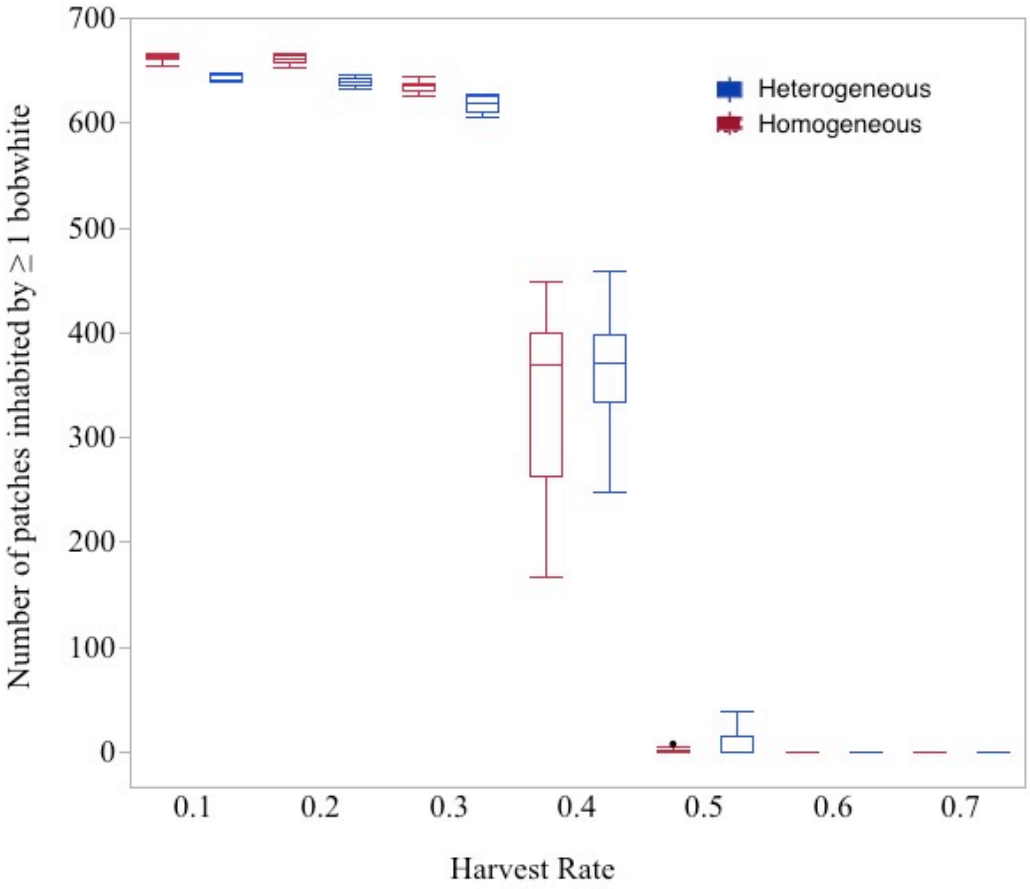

Number of patches inhabited by ≥1 bobwhite
700
600
500
400
300
200
100
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Harvest Rate
Heterogeneous
Homogeneous

Figure A2-9. BWD (A) and range (B) at t_{end} under the indicated dispersal rates in linear, baseline scenarios with no harvest. Boxes represent means (+/-1SE) and whiskers represent maximums and minimums of 100 Monte Carlo simulations.

Figure A2-9A

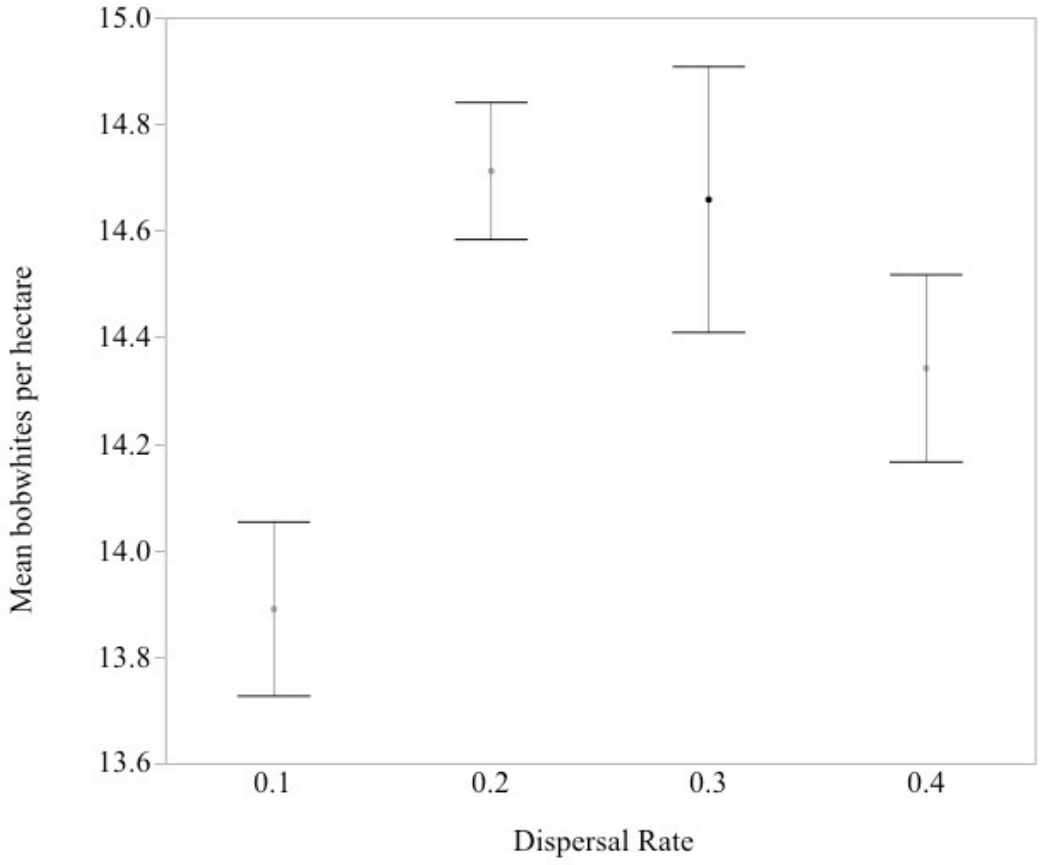


Figure A2-9B

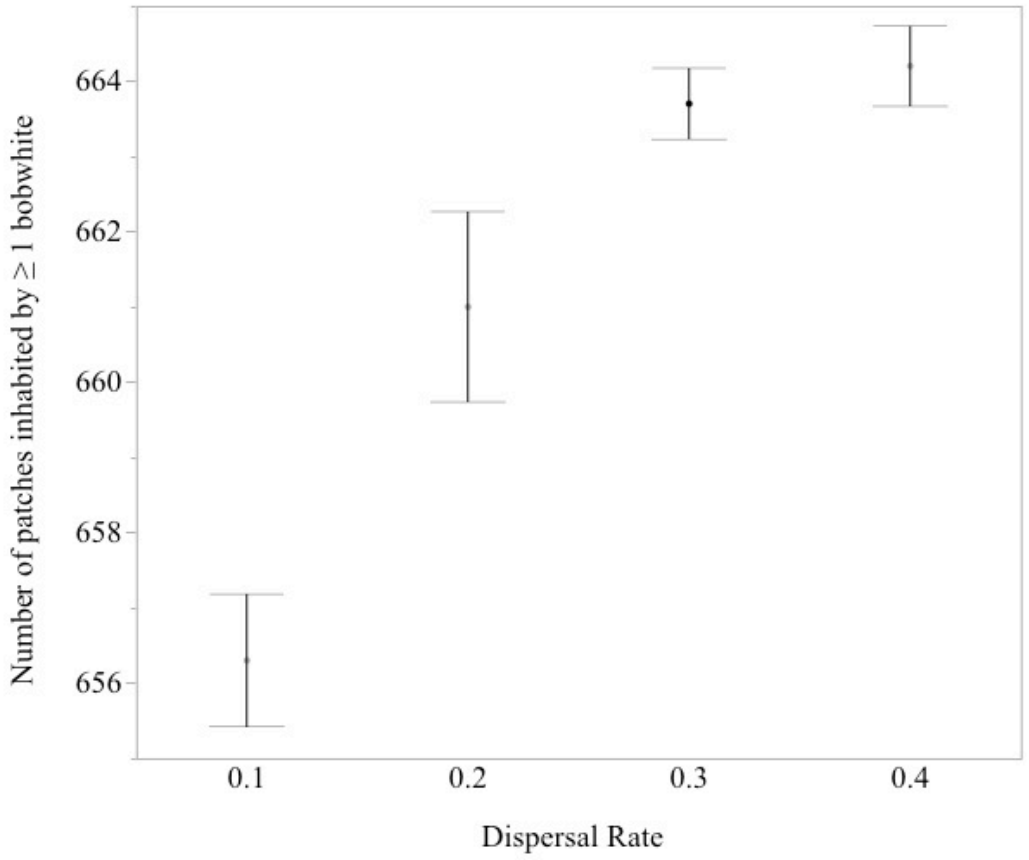

Number of patches inhabited by ≥ 1 bobwhite
664
662
660
658
656
0.1
0.2
0.3
0.4
Dispersal Rate

Figure A2-10. Density of bobwhites at t_{end} (after 100 years) under the indicated harvest and dispersal scenarios with 10% variation above and below mean harvest rates in spatially heterogeneous harvest levels, with hatch and mortality relationships to HQI in linear better (10A) and worse (10B), square baseline (10C), better (10D), and worse (10E) and square root baseline (10F), better (10G), and worse (10H). Boxes represent means (+/-1SE) and whiskers represent maximums and minimums of 3 Monte Carlo simulations.

Figure A2-10A

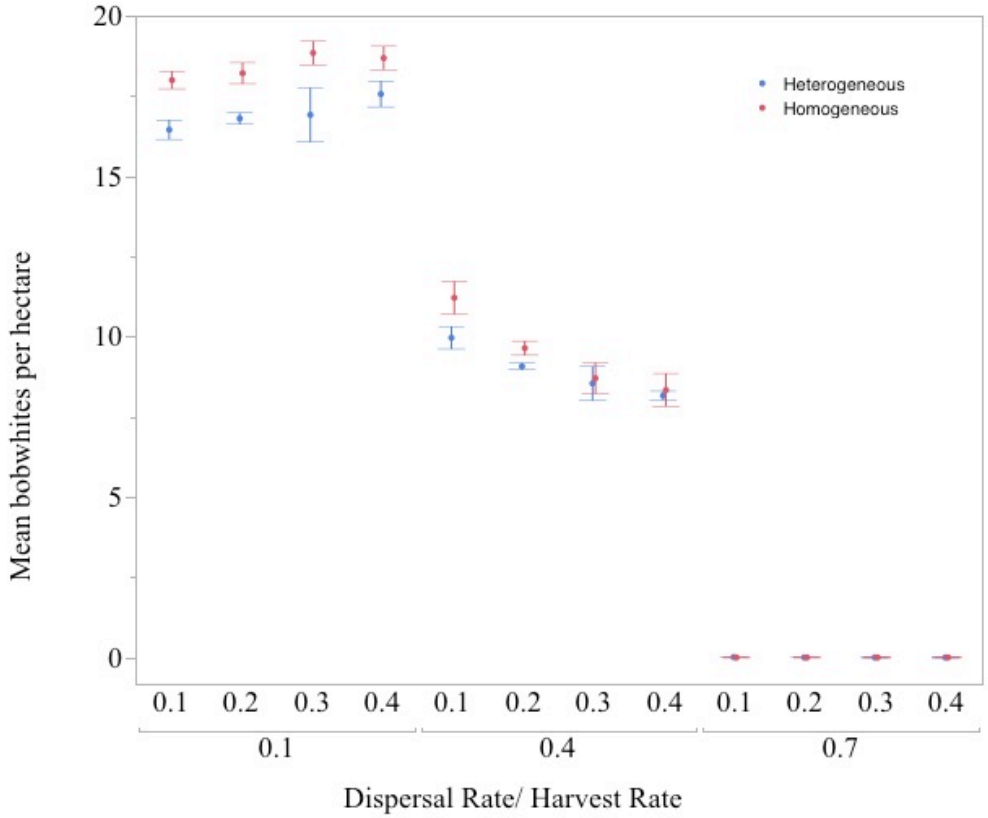


Figure A2-10B

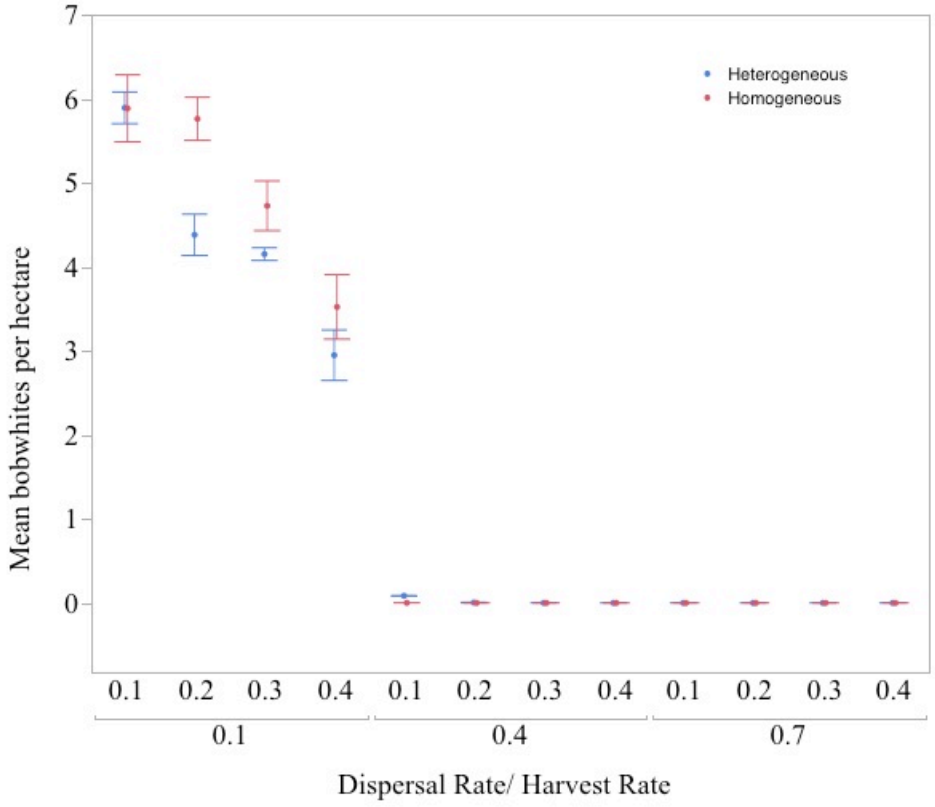


Figure A2-10C

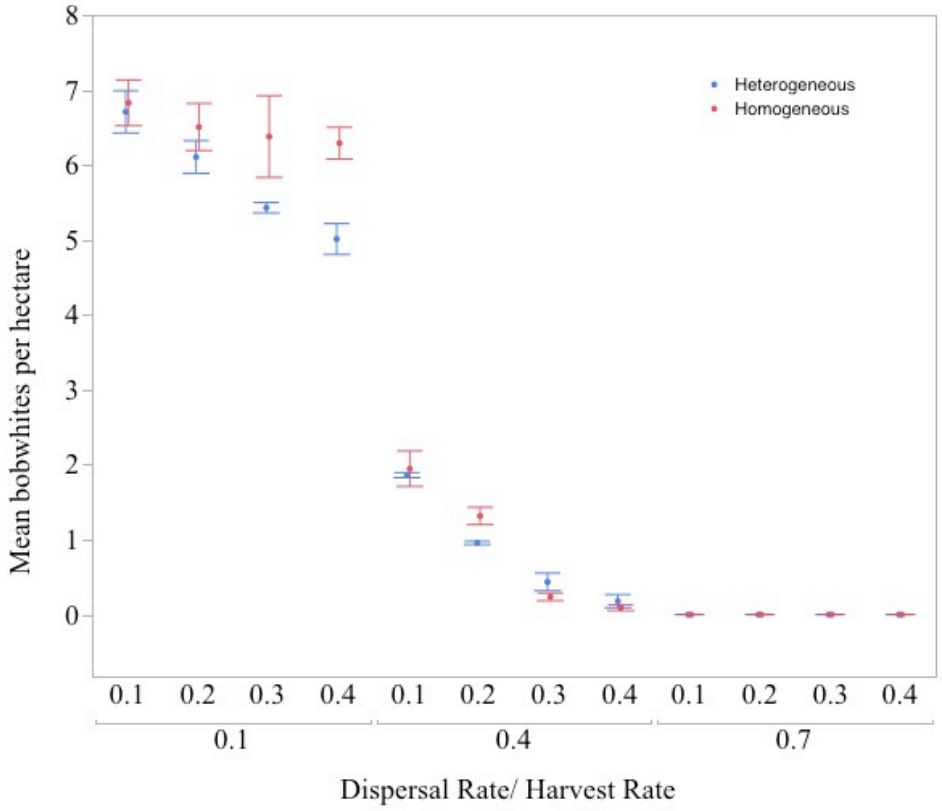


Figure A2-10D

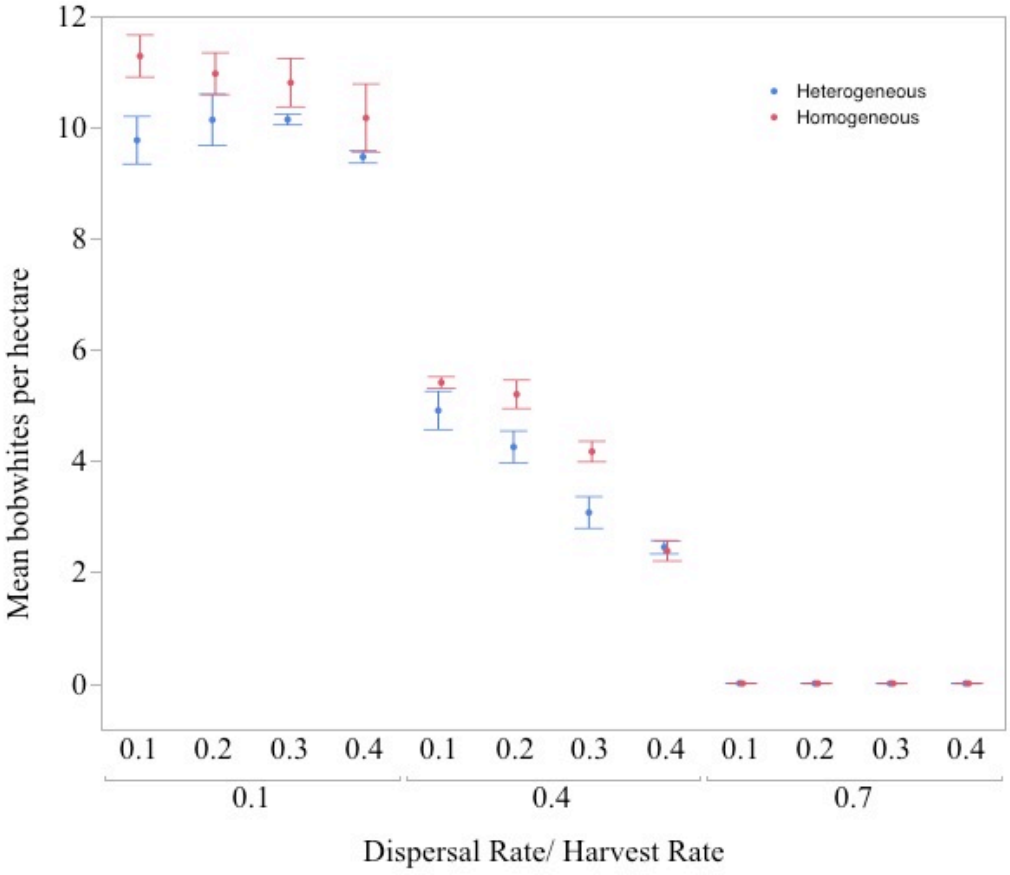


Figure A2-10E

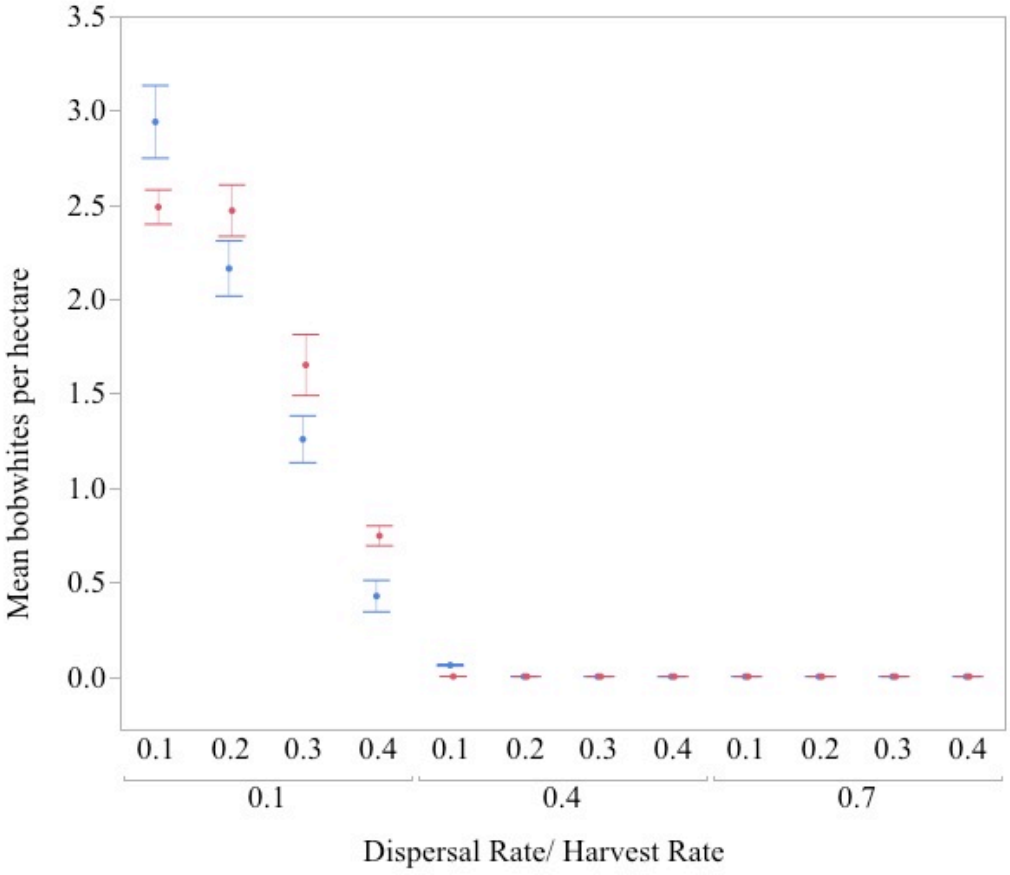


Figure A2-10F

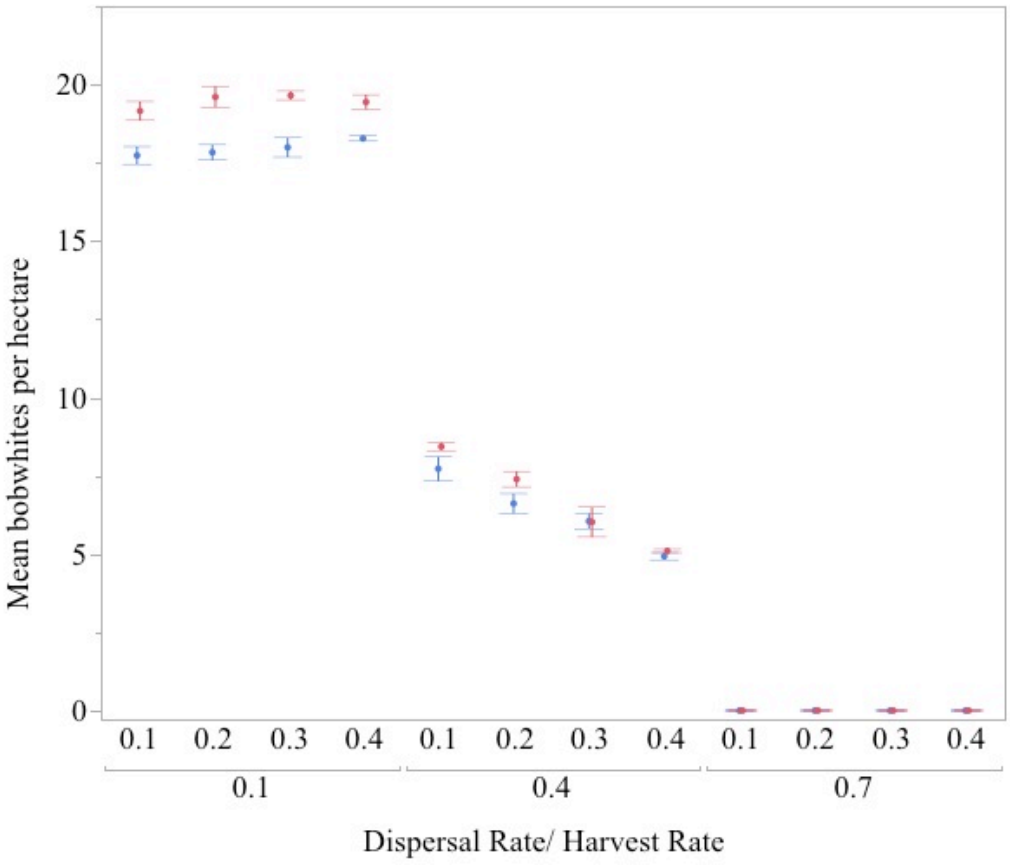


Figure A2-10G

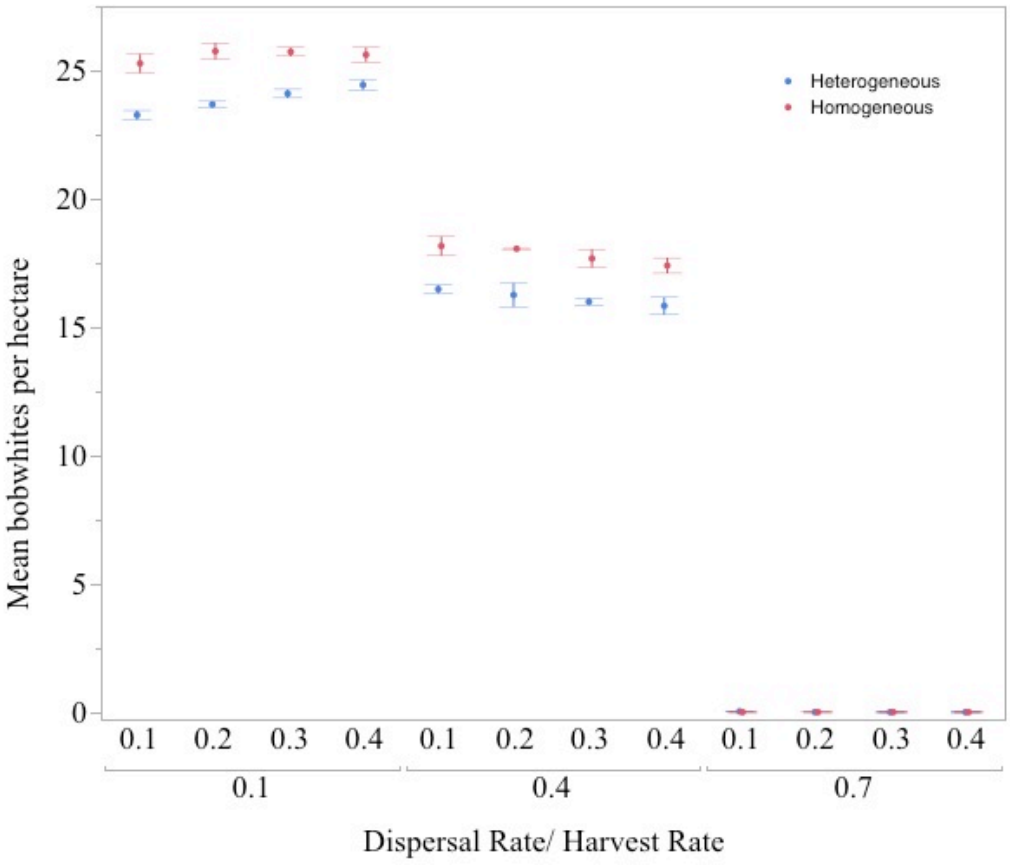


Figure A2-10H

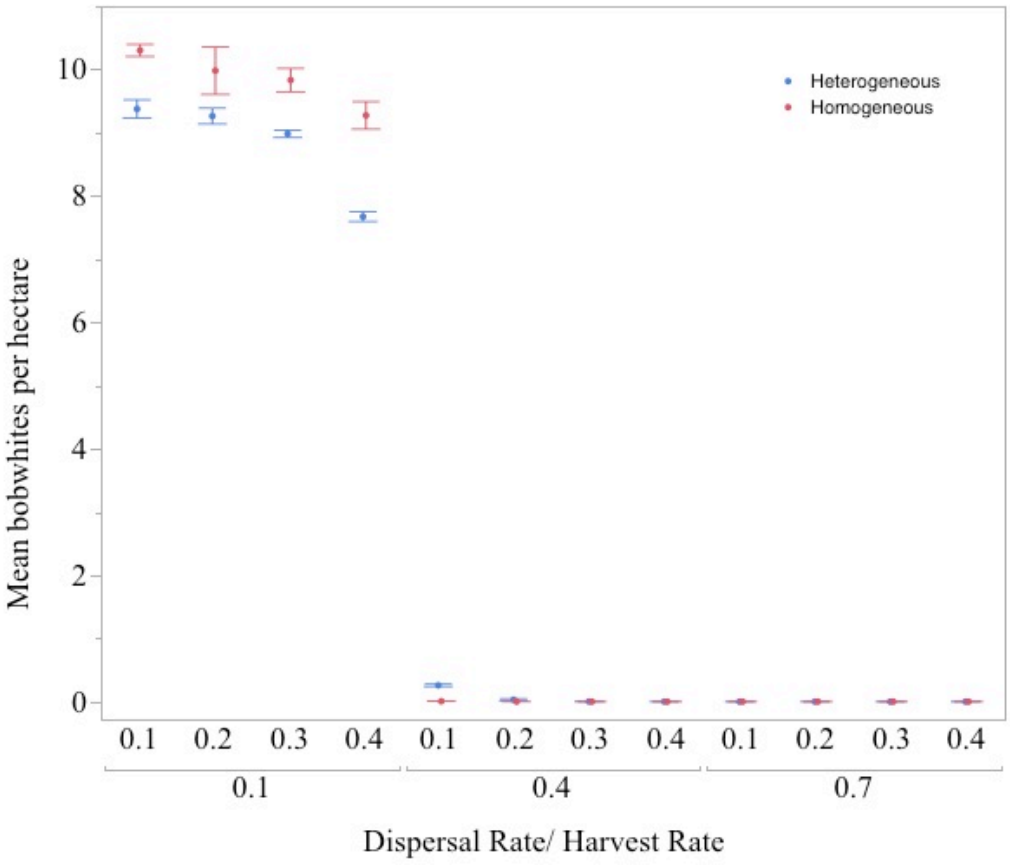


Figure A2-11. Number of patches inhabited by ≥ 1 bobwhite at t_{end} (after 100 years) under the indicated harvest and dispersal scenarios with 10% variation above and below mean harvest rates in spatially heterogeneous harvest levels, with Hatch and mortality relationships to HQI in linear better (11A) and worse (11B), square baseline (11C), better (11D), and worse (11E), and square root baseline (11F), better (11G), and worse (11H). Boxes represent means (+/-1SE) and whiskers represent maximums and minimums of 3 Monte Carlo simulations.

Figure A2-11A

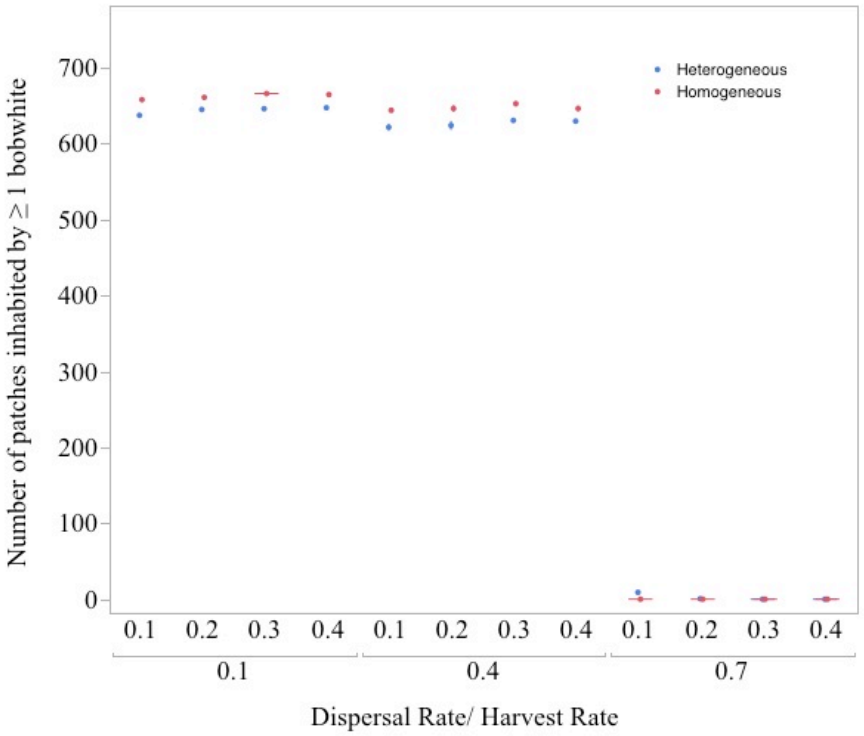


Figure A2-11B

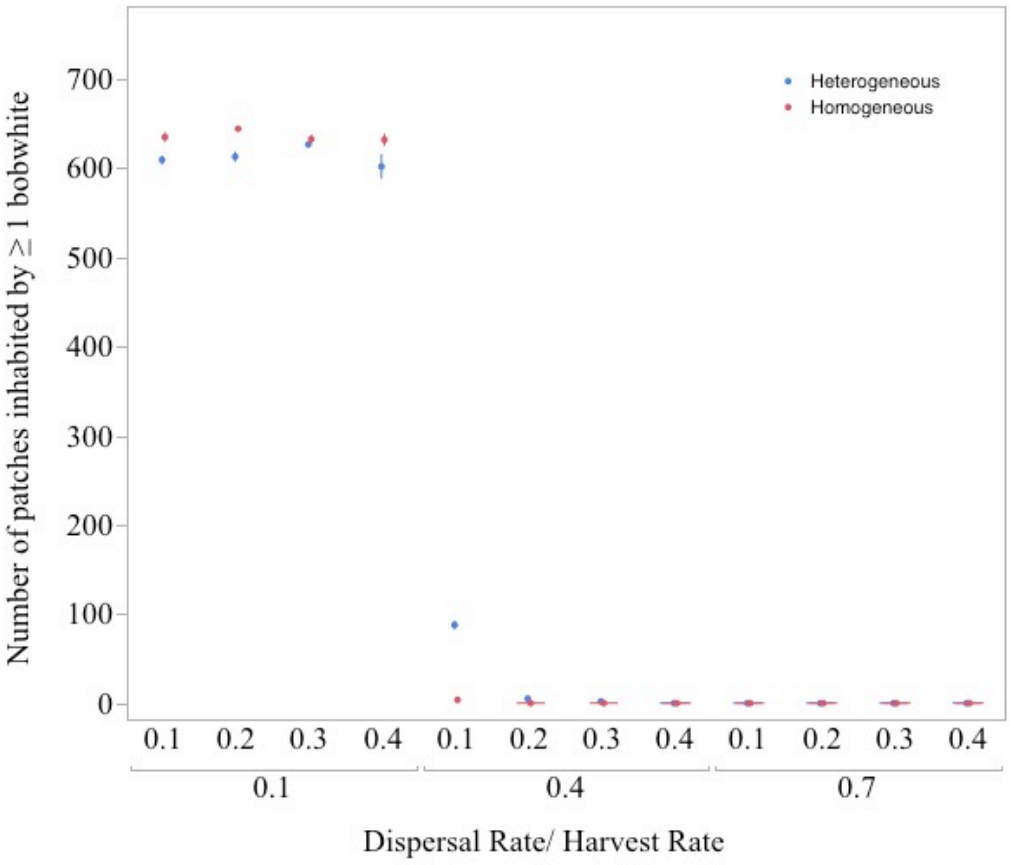


Figure A2-11C

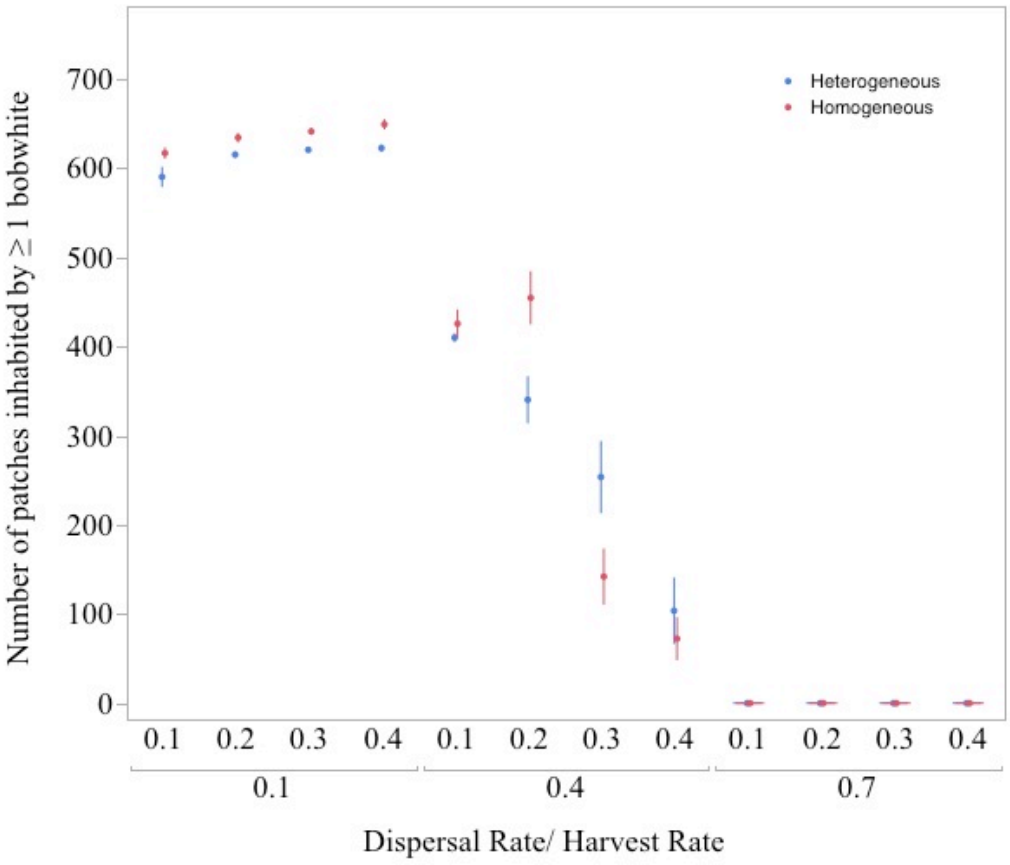


Figure A2-11D

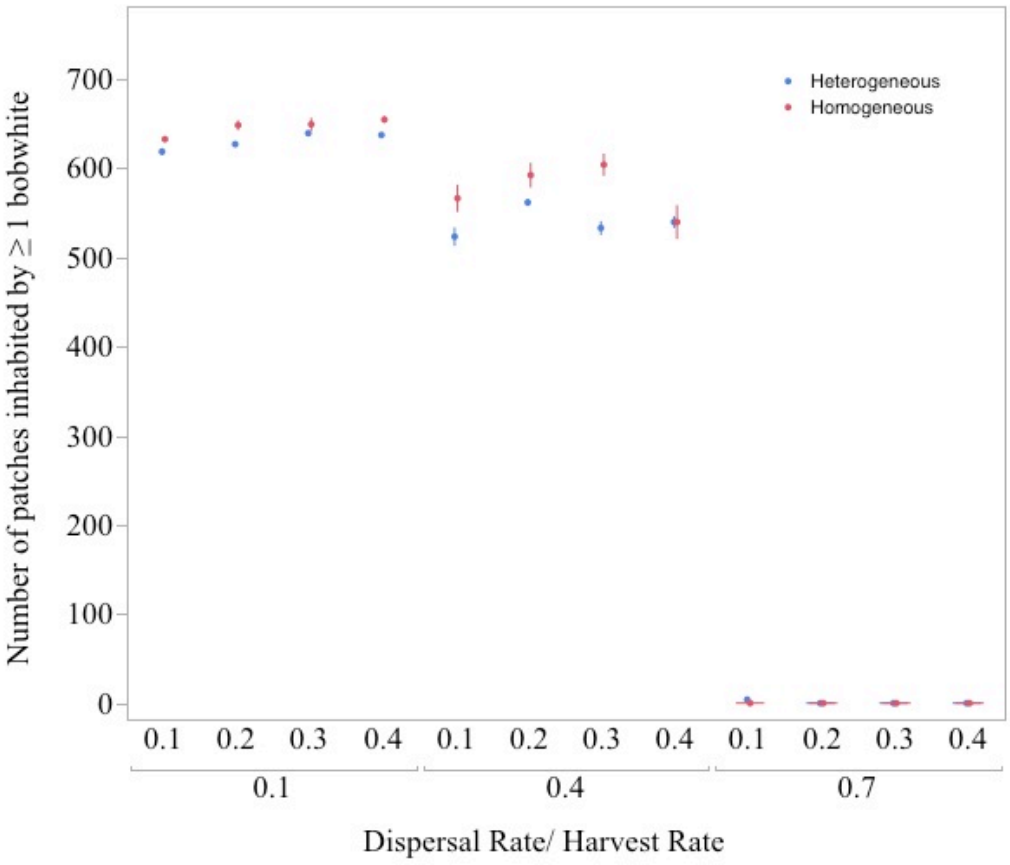


Figure A2-11E

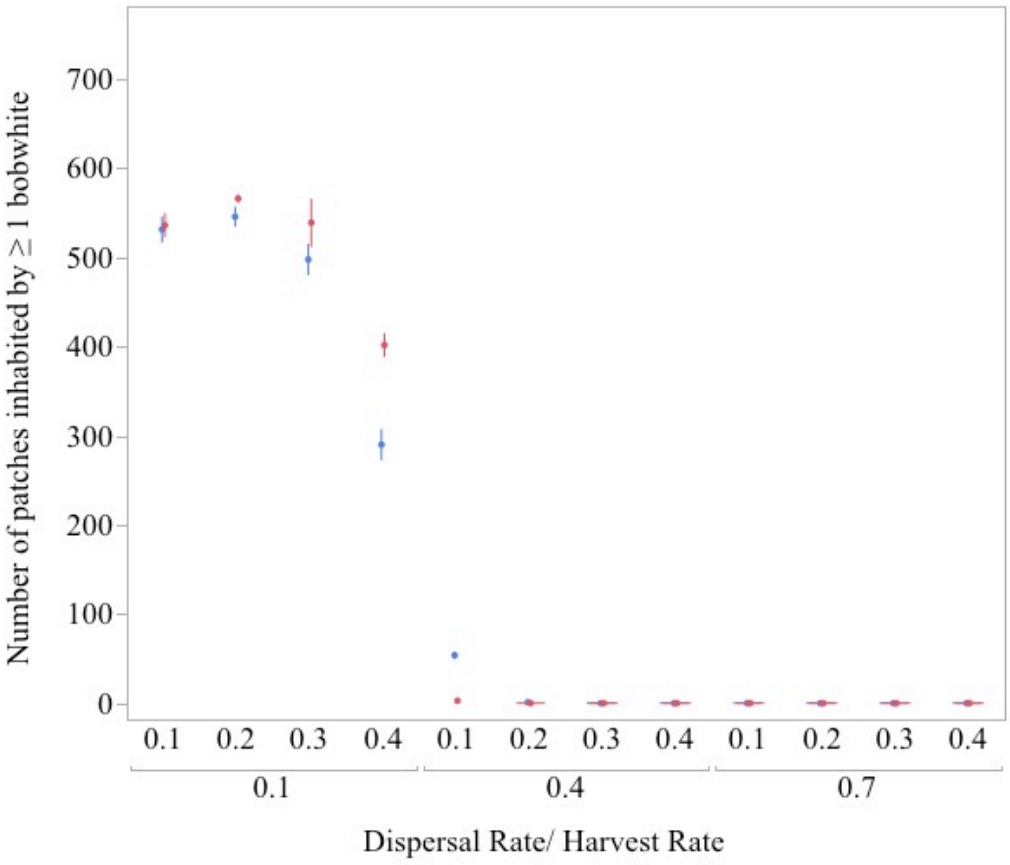


Figure A2-11F

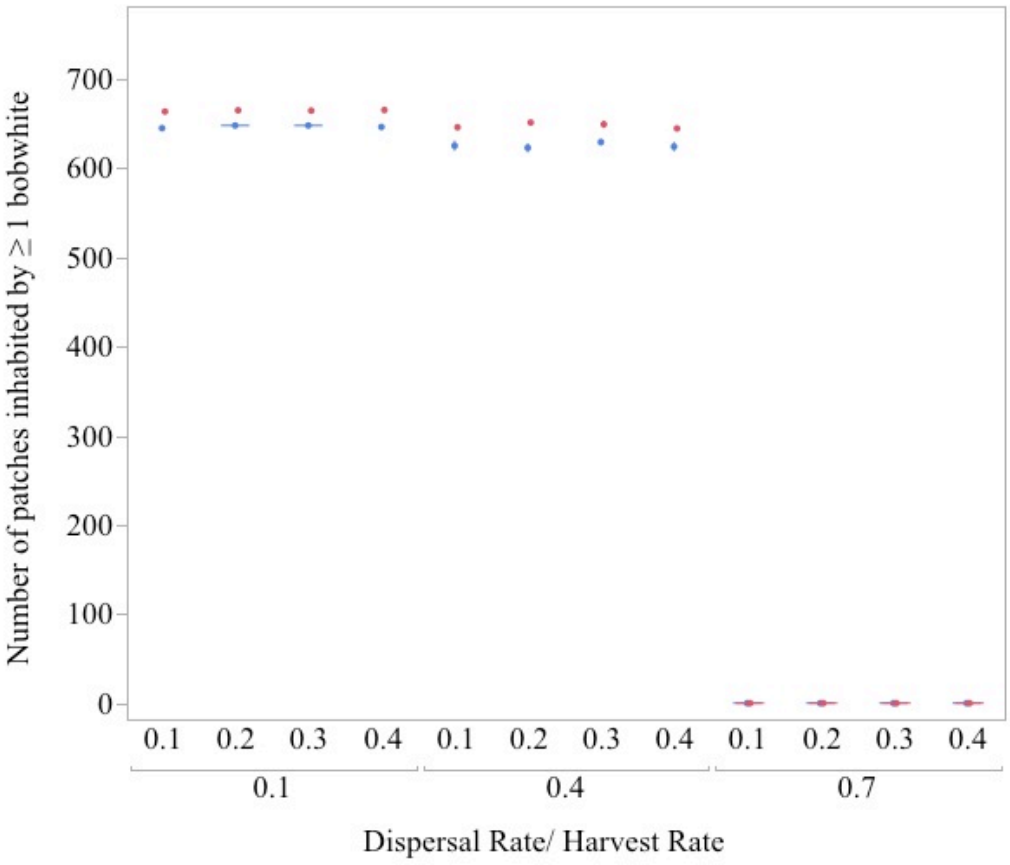


Figure A2-11G

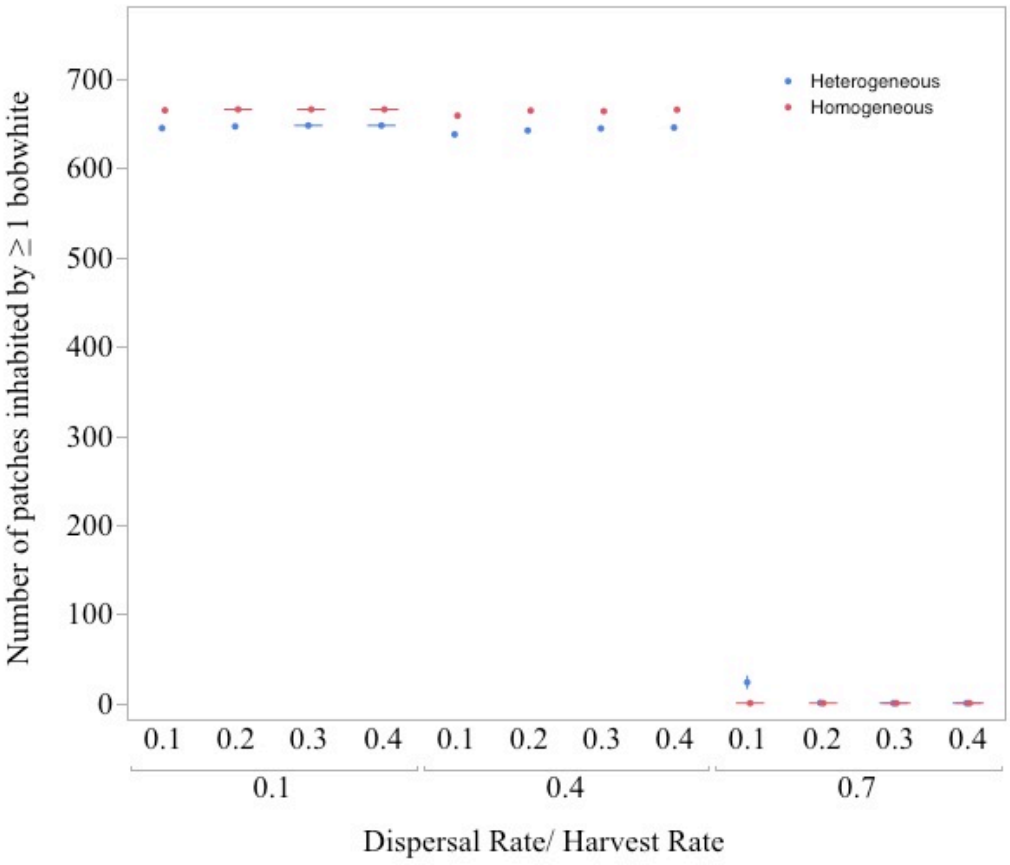


Figure A2-11H

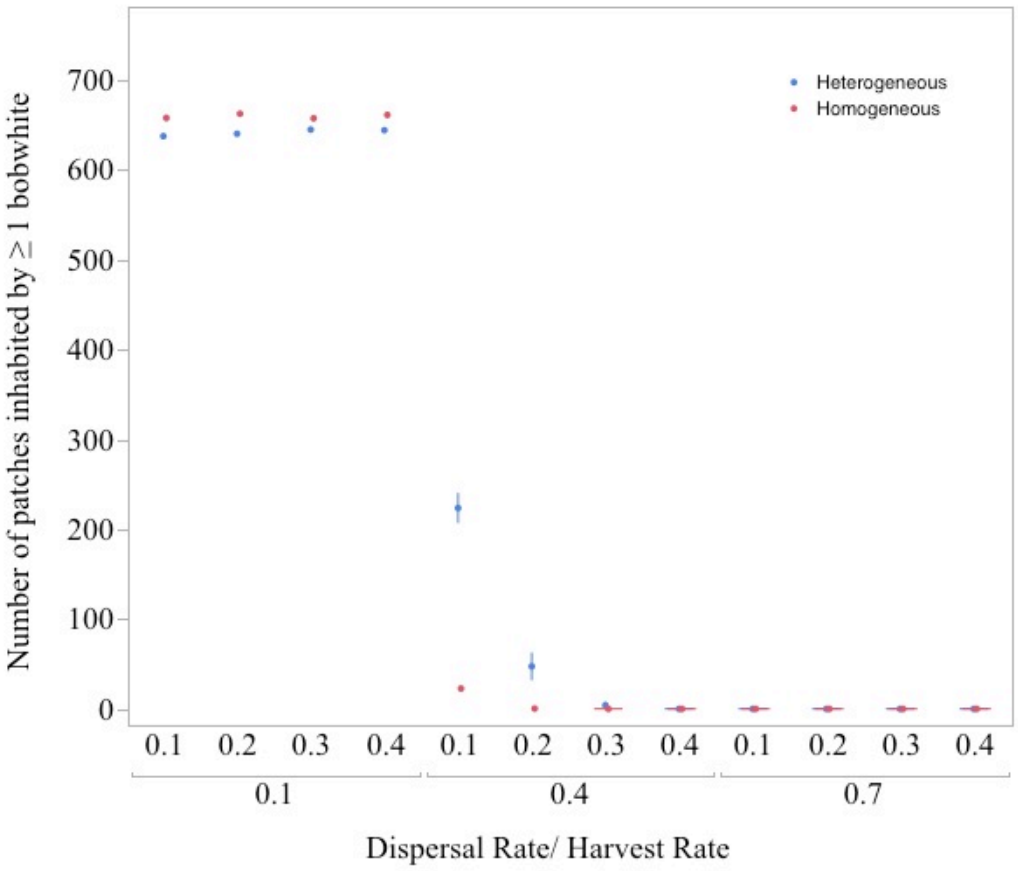


Figure A2-12. Diagram illustrating construction and insulation of mounted iButtons when viewed from the underside, specifically the (A) insulator mount, (B) foam pad, (C) iButton sensor, (D) white cable tie, and (E) attachment orifice to rebar electric fence post.

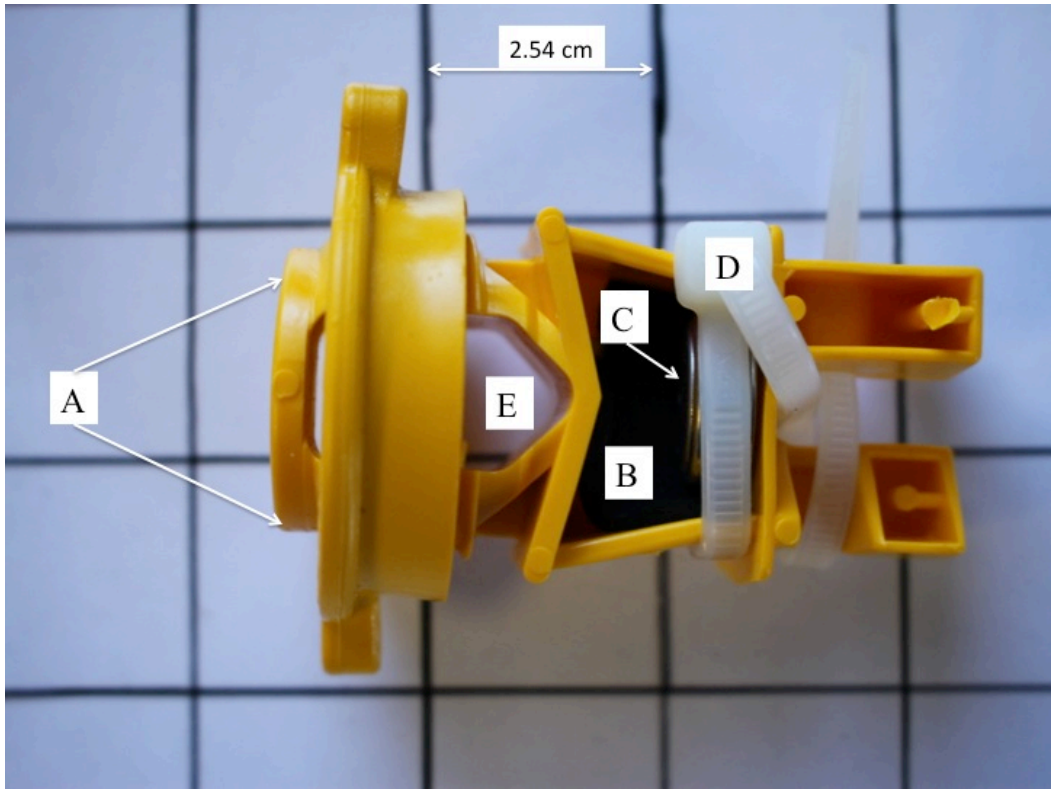


Figure A2-13. Photographs that give representative depictions of range conditions that I classified as (A) excellent, (B) moderate, or (C) poor for purposes of stratifying data based on relative bobwhite habitat condition.

Figure A2-13A

Figure A2-13B

Figure A2-13C

Figure A2-14. Monthly trends in mean temperature in bunch grasses suitable for bobwhite nesting cover and paired random points by sensor height (~10 cm and ~60 cm) during bobwhite nesting season (May–September) in the Rolling Plains of Texas, USA, 2012–2014

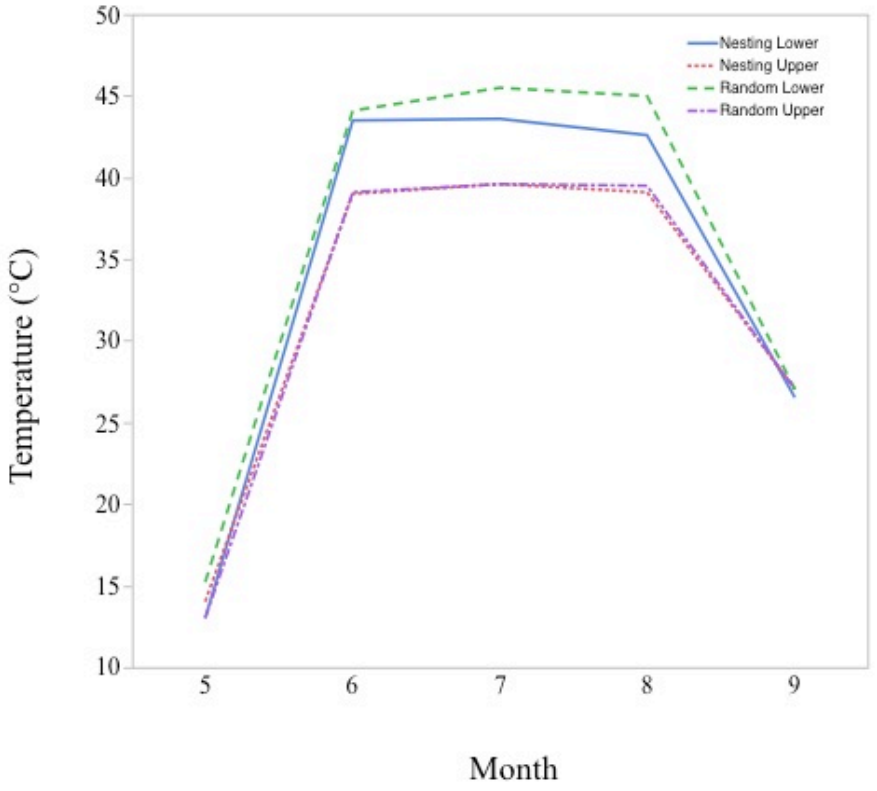


Figure A2-15. Monthly trends in mean percent relative humidity in bunch grasses suitable for bobwhite nesting cover and paired random points by sensor height (~10 cm and ~60 cm) during bobwhite nesting season (May–September) in the Rolling Plains of Texas, USA, 2012–2014

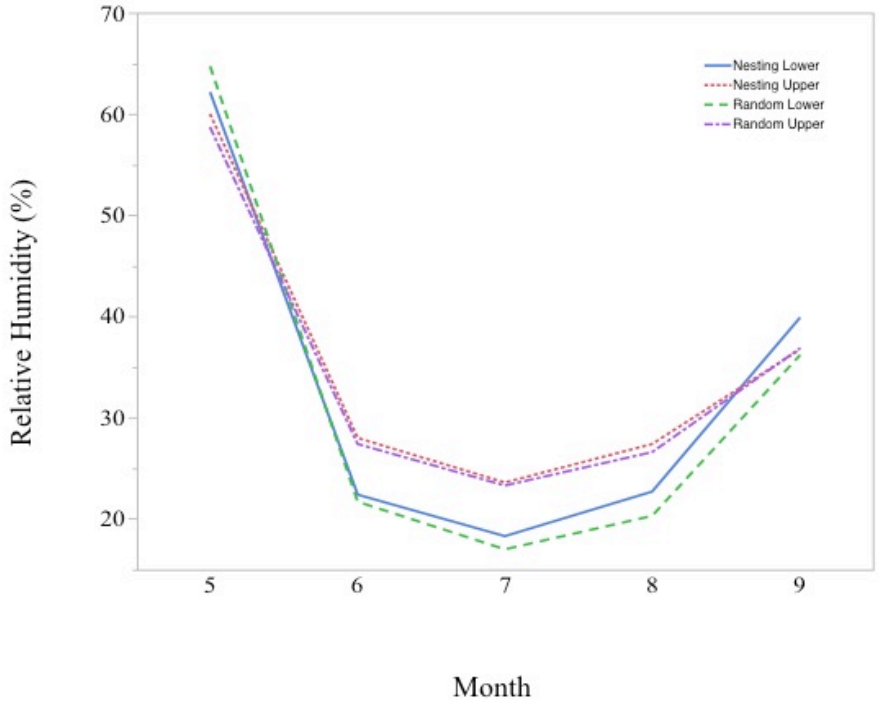


Figure A2-16. Monthly trends in mean temperature in bunch grasses suitable for bobwhite nesting cover and paired random points by sensor height (~10 cm and ~60 cm) during bobwhite nesting season (May–September) in the Rolling Plains of Texas, USA, 2012–2014. Harmful heat threshold (Reyna and Burggren 2012) indicated by line at 40°C.

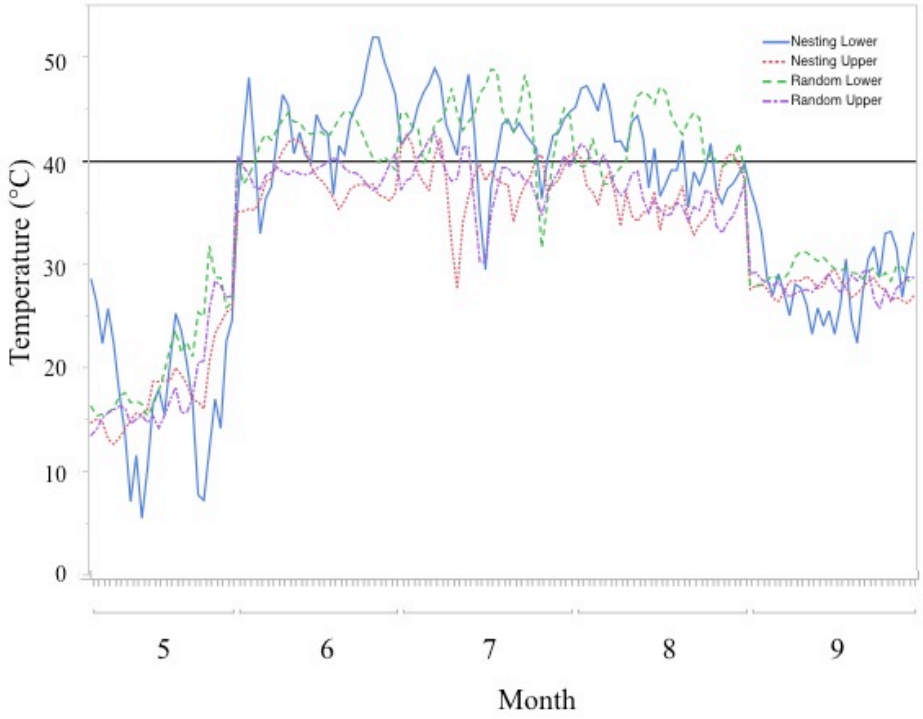


Figure A2-17. Monthly trends in mean percent relative humidity in bunch grasses suitable for bobwhite nesting cover and paired random points by sensor height (~10 cm and ~60 cm) at daily heat maxima during bobwhite nesting season (May–September) in the Rolling Plains of Texas, USA, 2012–2014

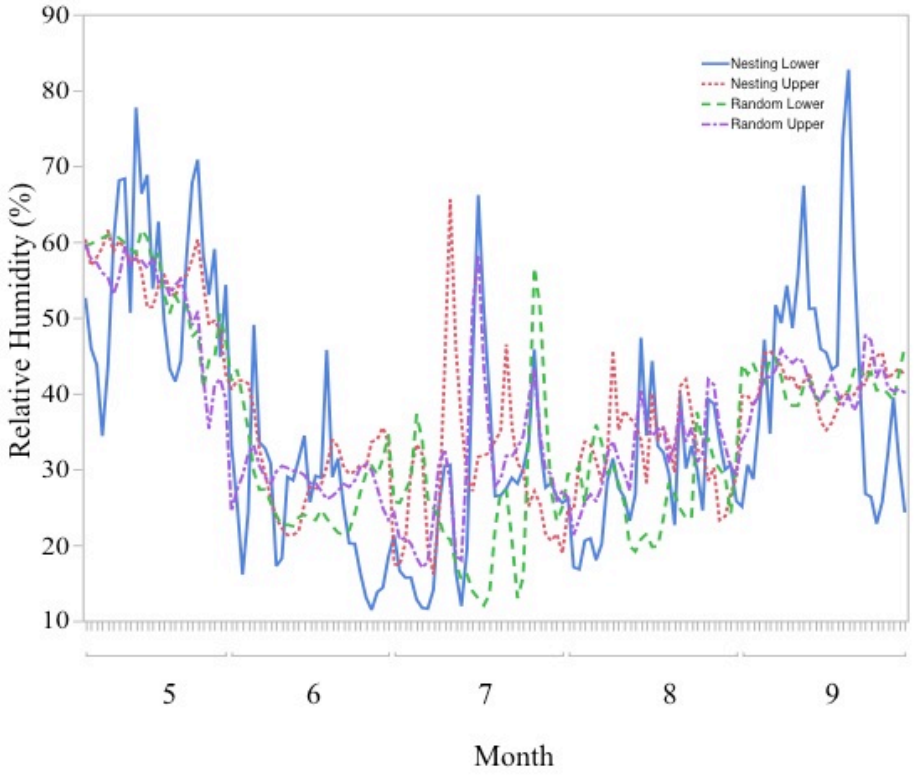


Figure A2-18. Daily trends in mean temperature in bunch grasses suitable for bobwhite nesting cover and paired random points by sensor height (~10 cm and ~60 cm) at daily heat maxima during bobwhite nesting season (May–September) on 3 ranches representing (A) excellent, (B) moderate, and (C) poor bobwhite habitat quality in the Rolling Plains of Texas, USA, 2012–2014. Harmful heat threshold (Reyna and Burggren 2012) indicated by line at 40°C.

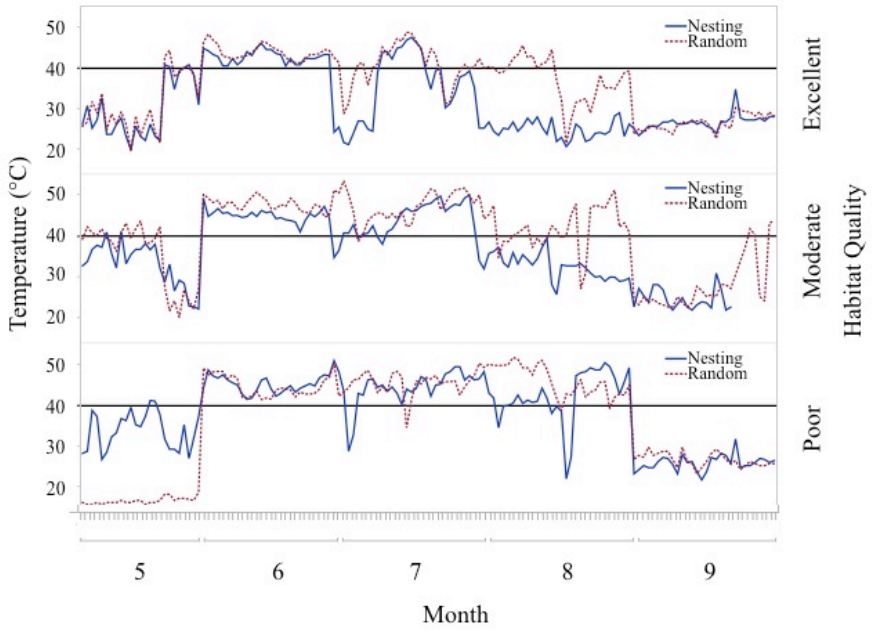


Figure A2-19. Daily trends in mean percent relative humidity in bunch grasses suitable for bobwhite nesting cover and paired random points by sensor height (~10 cm and ~60 cm) at daily heat maxima during bobwhite nesting season (May–September) on 3 ranches representing (A) excellent, (B) moderate, and (C) poor bobwhite habitat quality in the Rolling Plains of Texas, USA, 2012–2014.